

# EXTERNAL MORPHOLOGY OF ADULT SYRPHIDAE (DIPTERA)

by

M. C. D. SPEIGHT

Research Branch, Forest and Wildlife Service, Sidmonton Place, Bray, Co. Wicklow

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## INTRODUCTION

Dipteran morphology has been surprisingly little studied. Recent reviews of the available information are provided by McAlpine (1981) and in the sections on Diptera in the volumes by Bitsch et al. (1973), Bitsch & Matsuda (1979) and Matsuda (1965, 1970, 1976). From these texts conflicting theories as to the homologies of sclerites found in different Diptera are all too evident. And with the theories has grown

up a jungle of conflicting terminologies. Faced by the apparent inability of morphologists to agree on the morphological terms which can be applied to many of the taxonomically important parts of adult flies, and also finding need to refer to parts which to morphologists seemingly had no individual morphological identity, taxonomists have frequently been forced to coin quasi-morphological terms of their own. Workers on Syrphidae have been particularly plagued by this problem since morphologists have concentrated their efforts principally upon Nematocera and Calypterates, leaving Syrphid taxonomists to decide for themselves which of the sclerites found in Syrphidae could be identified with those named in other Diptera. The resulting terminological chaos reaches an extreme in accounts of European Syrphidae, where writers in different languages have developed partly independent terminologies but have also "borrowed" terms (sometimes in translation and sometimes not) from each other, adding to this mélange a sprinkling of polysyllabic latinisms when all else failed. At this juncture, it is doubtful that all Europeans working on Syrphidae would adopt in its entirety any proposed set of terms.

The present text does not attempt to select a definitive set! Certain principles have been employed here as follows:

- i) where the homology of a sclerite is generally agreed among morphologists and the sclerite is normally referred to in its entirety when used by taxonomists the latin (or greek) morphological term for the sclerite is used e.g. cercus;
- ii) where a sclerite has an agreed homology, morphologically, but is not normally referred to in its entirety in taxonomic texts, the terms used by taxonomists for each individual part of the sclerite are used if they

- are rendered in latin or greek and do not imply an *incorrect* homology for the sclerite e.g. post-alar callus;
- iii) where the homology of a sclerite is disputed but there is in existence for the sclerite a latin or greek term which does *not* imply a particular homology that term is used e.g. basale;
  - iv) where the homology of a sclerite is disputed and no suitable latin or greek term is available for that sclerite, a neutral term derived from some other language is used e.g. barrette.

The literature search conducted as part of the present work revealed only one complete published account of the external morphology of an adult Syrphid — the unillustrated text by Nayar (1965), on *Episyrphus balteatus*. Crampton (1942) considers the morphology of various Syrphids, but does not illustrate all the parts of any one species.

The present account is based on the morphology of the type species of the type genus of the family, *Syrphus ribesii* L., augmented by comparison with European representatives of the other two main subdivisions of the family, the Eristalinae (exemplified by *Eristalis tenax* L.) and the Microdontinae (exemplified by *Microdon mutabilis* (L.)). Other species are mentioned in discussion of particular parts of the fly, so that some idea can be presented of the range of morphological variation found among Palaearctic Syrphidae. Illustrations are all based on male specimens, except where specifically stated otherwise. In his massive work defining taxonomic subdivisions of the Syrphidae Hull (1949) illustrates a wide range of Syrphidae from different parts of the world, amply demonstrating the extremes of form exhibited by the family. His similar volume on fossil Syrphidae (Hull, 1945) gives an impression of the morphology of some of the family's antecedents. Studies of individual morphological regions or features of particular hoverfly species, or groups of species, have been undertaken by various authors. For instance, recently a favoured topic for consideration has been the male abdomen and the modifications undergone by its terminal segments. Such texts are mentioned in the relevant sections of the present account.

#### THE HEAD

Detailed morphological studies of the head capsule of *Eristalis* species have been conducted

by Gouin (1949) and Schiemenz (1957). Nayar (1964) considered *Episyrphus balteatus* and Crampton (1942) figured the head of a N. Amer. *Rhingia* species.

The major feature of the Syrphid head are the compound eyes and the mouthparts, which occupy, respectively, the lateral and ventral surfaces of the head capsule. The front of the head, from mouth-edge to ocellar triangle, is rather featureless, its main variation being in the extent to which it projects either ventrally to accommodate the mouthparts or dorsally to produce an antennal tubercle. The occipital region starts abruptly immediately behind the eyes, almost without exception forming a sharp angle with the sides of the head.

As Snodgrass (1960) has pointed out there is a great difference between joints between sclerites (Sutures) and intrascleritic invaginations of the exoskeleton (Sulci) that form sites for muscle attachment, but these two phenomena can be indistinguishable externally. In Syrphids the head capsule exhibits on its surface various grooves marking the location of internal apodemes and most authors referred to these grooves as "sutures", thus not differentiating them from features representing joint lines. In order to make the necessary distinction, these cephalic grooves are here called sulci, following Snodgrass's (l.c.) terminology.

#### Compound eyes

In Syrphids the two compound eyes are large, occupying most of the top and sides of the head and making up two thirds or more of the width of the head capsule. There is a certain amount of sexual dimorphism, the male eyes meeting in the mid-line between antennal insertions and ocellar triangle (the holoptic condition) in a majority of the genera, but always remaining separate (the dichoptic condition) in the females (figs. 1, 2). In addition, facets in the upper part of the male eyes may be distinctly larger than those below (e.g. in *Scaeva*) while in the female they are of very similar dimensions throughout. Short, straight hairs, inserted between the facets, characterise some genera. These hairs may be generally distributed over most of the surface (as in many *Cheilosia* species) or arranged in stripes of different density (as in *Eristalis tenax*) or colour (as in *Paragus* species). In some genera the facets themselves iridesce in bands or spots of different colours (as in *Eristalodes*, *Orthonevra* and *Eristalinus*) which fade after death. Some authors, e.g. Gouin (1949), have recognised

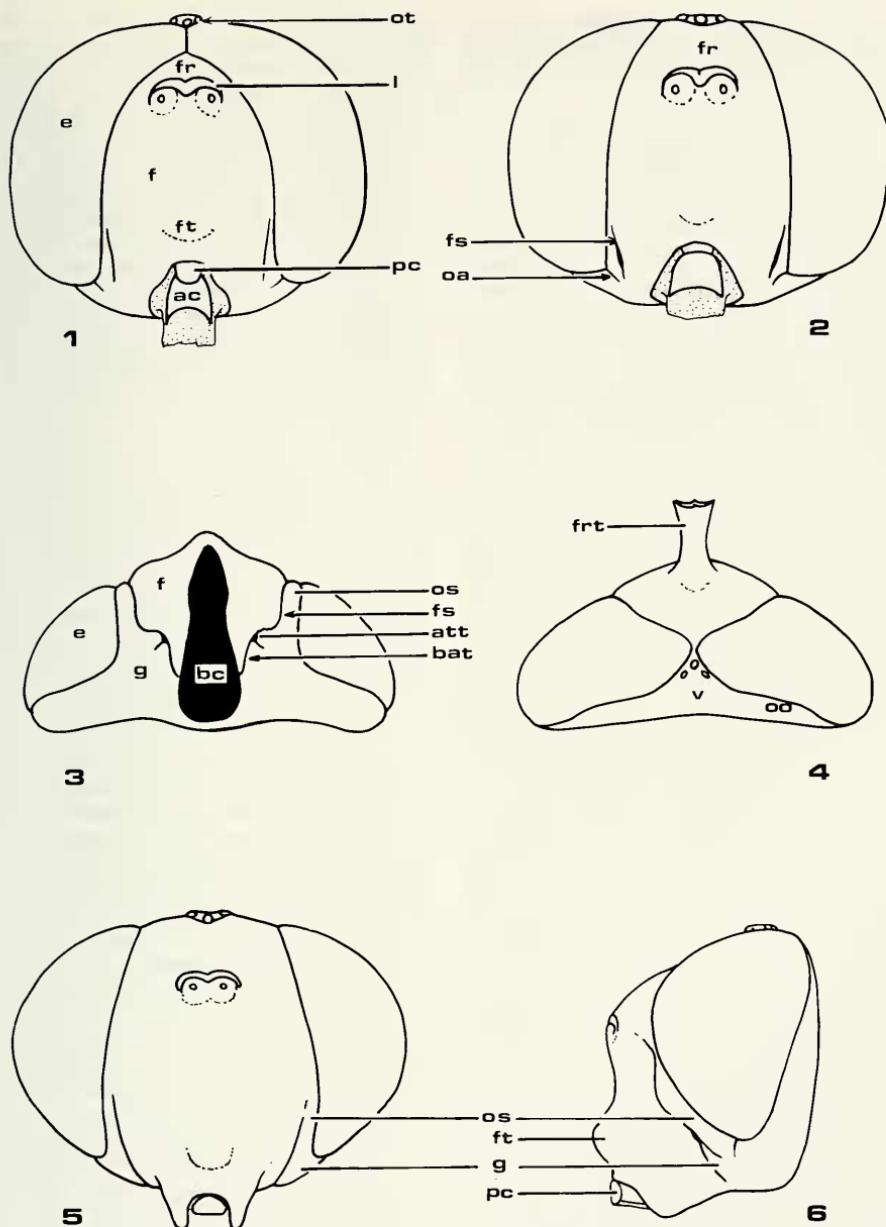


Fig. 1, *Syrphus ribesii*, male, head, anterior view. Figs. 2, 3, *S. ribesii*, female, head, anterior view (2) and ventral view (3). Fig. 4, *Ceriana* sp., male, head, dorsal view. Fig. 5, *Eristalis tenax*, female, head, anterior view. Fig. 6, *Cheilosia grossa*, male, head, lateral view of left side.

an externally visible ocular sclerite forming a rim to the eyes, but no external evidence of this plate has been encountered by the present author.

#### Head capsule: frontal, genal and vertical regions

Sulci precisely delimiting the frons are absent in Syrphidae, leaving the anterior ocellus, the compound eyes and the anterior tentorial pits as the only reference points by which to define the extent of the frontal region of the head capsule. Judged in this way, the "frons" is generally regarded as extending from the ocelli to the anterior rim of the buccal cavity. The clypeus, which should intrude between frons and mouth-parts is taken either to have disappeared, or to have been incorporated without trace into the lower areas of the frons, or (as in most recent literature) to have been mostly incorporated into the buccal cavity. Most authors have failed to refer to the area from the antennae to the edge of the buccal cavity as the frons, restricting this term to the area between antennae and ocellar triangle (the term ocellar triangle refers, as used here, to the often raised triangular area containing and demarcated by the ocelli). The lower frons is then referred to as either the face (as in McAlpine, 1981) or the fronto-clypeus. In some instances the area immediately above the edge of the buccal cavity is termed the post-clypeus, on the assumption that only the more basal of the two clypeal plates has been absorbed into the frons. Since there are median sclerites in the front part of the buccal cavity (see section on mouthparts) serving the functions which sclerites of the clypeal origin might be expected to serve and since the more basal of these is hinged to the upper edge of the buccal cavity, it seems unreasonable to regard them as secondary sclerites and thus require the true clypeus to have been incorporated without trace into the frons. Following this logic the entire area between anterior ocellus and the upper mouth edge is here regarded morphologically as the frons.

However, there is taxonomically a need to distinguish between the frontal area above the antennae and the frontal area beneath them, so following popular usage the latter area is referred to here as the *face* (this does not entirely accord with the definition of the face used in McAlpine, 1981, where the face is taken to terminate below the level of anterior tentorial pits) and the former as the "frons".

A dorsal-ventral sulcus continuing upwards on

each side of the lower frons, from the invagination of each anterior tentorial pit, and more or less parallel with the anterior eye margin, is developed to a greater or lesser extent in many Syrphid genera. This facial sulcus is almost universally well-developed in *Cheilosia* spp (fig. 6), where it reaches the level of the antennal insertions. In this way, the part of the face between the facial sulcus and the eye margin is cut off from the rest of the face and also frequently looks very different, due to differences in colour and pilosity between it and the rest of the face. Some authors have sought to name these orbital strips as separate regions of the head capsule, labelling them *genae* or *parafrontalia*, etc. Here they are simply termed the *orbital strips* (figs. 3, 5, 6).

At its ventral end the tentorial sulcus does not terminate precisely at the anterior tentorial pit (usually detectable externally as a widening and deepening of the sulcus) and may bifurcate, one arm (buccal arm) continuing to the edge of the buccal cavity, the other arm (ocular arm) swinging round towards the antero-ventral angle of the eye, where it slopes at the eye margin. Either or both of these arms may be incomplete. In *Syrphus* (figs. 1, 2) both arms are incomplete, but in genera where the ocular arm is complete externally and the buccal arm is not in evidence (e.g. in *Cheilosia*, fig. 6) the orbital strips are delimited precisely at their lower ends. In *Eristalis* (figs. 3, 5), where the ocular arm is indistinct but the buccal arm continuous strongly to the edge of the buccal cavity, the buccal arms divide the face into a median and lateral regions. Schiemenz (l.c.) regards these lateral regions as the *genae* and in those Syrphidae in which both lower arms of the anterior tentorial sulcus are complete this use of the term would follow precisely the definition of the *genae* given by Snodgrass (1960). Where one or other, or both, lower arms of the anterior tentorial sulcus are missing the frontal and genal regions of the head capsule cannot, by definition, be precisely delimited.

The antennal insertions are found on the frons. Immediately above them a pair of arcuate raised areas is usually differentiated (absent in *Microdon*) in Syrphidae. These are jointly known as the *frontal lunule*. That part of the top of the head capsule between the para-sagittal sulci (fig. 7) and containing the ocellar triangle with its three ocelli is most conveniently referred to as the *vertex*. Crampton (l.c.) has discussed the difficulties inherent in using this term in Diptera. Here the vertex is taken to merge imperceptibly

with the occipital region of the head capsule at the angle where the posterior face of the head dips down. Gouin (l.c.) and Schiemenz (l.c.) used the terms *vertex* to include the median part of the occipital region referred to here as the *post-vertex*. Other authors have used the terms "vertex" and "vertical triangle" as synonyms of the term "ocellar triangle" as employed here. It should be noted that in the males of the syrphid species with holoptic eyes the vertex is frequently represented only by the area of the ocellar triangle, such that the terms *vertex* and *ocellar triangle* become interchangeable, giving rise to some confusion. In both sexes of most species the ocelli are disposed in a roughly equilateral triangle. But in some genera e.g. *Eumerus*, species occur in which the anterior ocellus is placed further forward, some distance from the two lateral ocelli.

Dorsally, behind the eyes and lateral to the vertex, the head capsule often projects to some extent, before curving ventrally into the occipital region. Whether or not there is a para-sagittal sulcus in evidence on each side of the ocellar triangle, thus precisely segregating the vertex from these post-ocular strips, they may conveniently be termed the *post-ocular orbits*, as in Coe (1953). The post-ocular orbits continue without interruption down the side of the head to merge with the genal region.

Between the antennae and the upper mouth edge a median protruberance is present in many Syrphid genera. Although this bump has no discrete identity morphologically, it is important taxonomically and is usually referred to either as the *facial tubercle* or *facial prominence* (figs. 1, 6). The area surrounding the antennal insertions may also be drawn out to form a tubercle, which in European Syrphids reaches its extreme of development in *Ceriana* (fig. 4). This has been referred to as the *frontal prominence* or *frontal tubercle*.

The surface of the frons is not infrequently thrown into a series of furrows or ridges (referred to as *regulae*) well illustrated by species of *Chryogaster* and *Orthonevra*. Other genera exhibit highly polished concave or flattened median fields contrasting markedly with the surrounding surface, e.g. *Neoascia* and *Neocnemodon*, or areas of procumbent, iridescent microhairs (dusting) alternating with bare, shining patches, as in many Syrphinae.

#### Head capsule: posterior surface

In Syrphidae, the posterior surface of the head

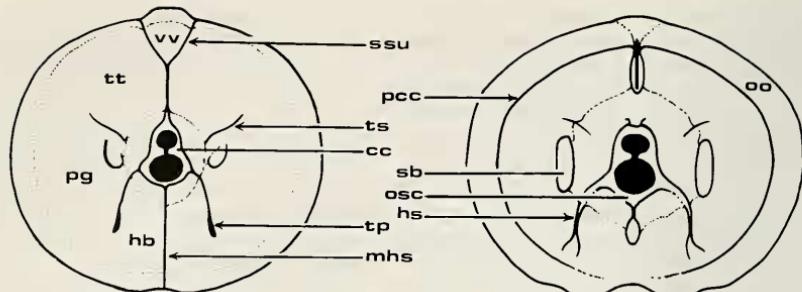
(*post cranium* of McAlpine, l.c.) is concave, making a sharp angle with the sides of the head. In the case of *Eumerus* and *Merodon* this angle is extremely sharp, producing a distinct postcranial carina (fig. 8). This angle makes a very convenient marker for defining the outer edge of the three major post-cephalic regions, referred to here as the *occipital region*, the *post-genal region* and the *hypostomal region*. Tentorial sulci, radiating out from the centre, delimit these regions one from another.

More or less in the centre of the back of the head is found the *occipital foramen*, or foramen magnum. This is largely surrounded by the *post-occipital sclerite*, which merges below with a mid-ventral plate delimited laterally by the well-marked *hypostomal sulci*. This mid-ventral plate makes up the hypostomal region of the head and is supposedly derived largely from lobes of the postgenae that have fused in the mid-line (Snodgrass, l.c.) giving it one of its names, the *hypostomal bridge*. In *Syrphus* and its allies (fig. 7) a dorso-ventral, median, hypostomal suture probably indicates the fusion line. The posterior tentorial pits occur in the hypostomal sulci and the two lateral plates demarcated ventrally by the hypostomal sulci make up the *post-genal region* (referred to simply as a part of the genae by Gouin and Schiemenz) of the head. A more dorsal pair of rather incomplete sulci, referred to as the *transverse sulci*, help to delimit the upper boundary of the postgenal region. The *occipital region* is then that part dorsal to the transverse sulci. Yet another pair of sulci, the *parasagittal sulci*, divide the occipital region into three fields. The two lateral fields of the occipital region have usually been called the *tempora* but the dorsal, median, field has been subject to various appellations. Here it is termed the *post-vertex*. In *Merodon* and related genera the post-vertex is almost obliterated (fig. 8), the para-sagittal sulci swinging into the mid-line at the post-cranial carina.

Very prominent towards the centre of the postgenal fields of Eristaline syrphids are large, raised, dorso-ventral bands of sensillae — these bands of sensillae are often very restricted in their extent in Syrphinae. In all Syrphids the occipital foramen is so constructed just above mid-way as to be almost converted into two separate holes, due to the development of prominent transverse *cervical condyles* for articulation with the cervical sclerites (figs. 7, 8).

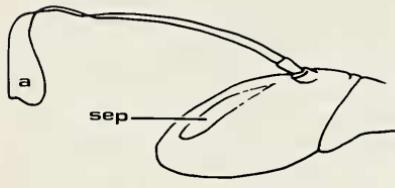
#### Antennae

Syrphid antennae comprise three principal

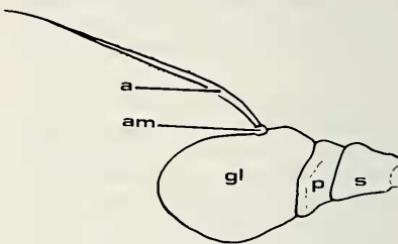


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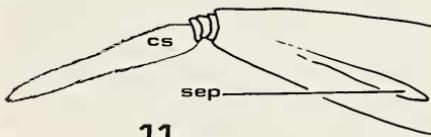
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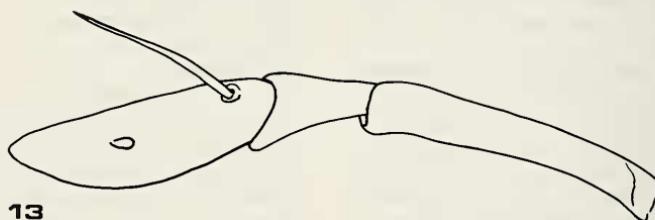
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Fig. 7, *Syrphus ribesii*, male, head, posterior view. Fig. 8, *Merodon equestris*, male, head, posterior view. Fig. 9, *Platynocheaetus setosus*, third antennal segment and arista, lateral view, outer side. Fig. 11, *Callicera aenea*, end of third antennal segment and arista, lateral view, inner side. Fig. 12, *Syrphus ribesii*, antenna, lateral view, inner side. Fig. 13, *Microdon mutabilis*, antenna, lateral view, outer side.

segments and a more or less annulate *arista* borne on the third segment. The third segment represents the first flagellar segment. The arista represents the rest of the flagellar segments, one or more of which may be distinct (figs. 9—13). These aristal segments have been termed aristomeres (McAlpine, l.c.). Inserted between the eyes on the frons, the antennae occur at a point where there is a distinct change in the angle of slope of the frons. Not infrequently the frons projects at this point, producing in extreme cases a frontal tubercle (fig. 4).

The antennal segments vary in their proportions between genera, but segment 3 is normally the largest. Sensory pits are frequently discernible on either the inner or the outer face of segment 3. *Cheilosia* species often possess large numbers of small pits, while in many other genera there is at least one large pit (figs. 9, 11, 13). The dorsal margins of segments 1 and 2 carry bristles in various genera.

The arista may be terminal or sub-dorsal, hairless, pilose or plumose. In most genera it is bristle-like, but it may be bulbous or strap-like. In *Platynocheilus* it is spatulate (fig. 9). Crampton (1942) discusses the merits of applying the term "ceratostylate" to certain forms of the antennae with a terminal "arista" and the condition found in *Ceriana* would certainly be better termed cerato-stylate rather than aristate were the term ceratostyle to come into common use.

To accord with general usage, the terms *scape* and *pedicel* should be applied to the first and second antennal segments, respectively.

### Mouthparts

The modifications exhibited by the mouthparts of Syrphidae, occasioned by these flies' specialised nectar and pollen-feeding habits, have given rise to various published accounts of their structure. The most detailed study is that of Schiemenz (1957), who deals with both external and internal anatomy of the mouthparts of *Eristalis arbustorum*. Crampton (l.c.), Gilbert (1981), Gouin (l.c.), Holloway (1976) and Nayar (1964) provide additional information. Gilbert's (l.c.) account considers the functional implications of variations in structure exhibited by a range of European species and also incorporates a comprehensive bibliography.

Although morphologically part of the head-capsule the clypeal sclerites have apparently come to lie within the buccal cavity in Syrphidae, so they are considered in this section of the present text together with the head appendages

which make up the mouth-parts proper (alternative theories concerning the fate of the clypeus are mentioned under the section dealing with the frons).

Syrphid mouthparts comprise sclerites derived from the clypeus, located dorsally towards the base of the mouthparts complex; a modified *labrum* lying dorsally and distal to the clypeal sclerites; a lateral pair of *maxillary stylets* plus palps; a ventral *hypopharynx* and a partly membranous and partly sclerotised labial complex lying beneath the hypopharynx. The labial complex provides a sheathing trough (the "labial gutter") for the other mouthparts that lie distal to the clypeal sclerites. The entire apparatus, normally called the proboscis, is hinged to the head capsule at the upper mouth edge, via the basal clypeal sclerite, and hinged again at the junction between the distal clypeal sclerite and the labrum. Because of this hinging arrangement, when the proboscis is retracted into the head it folds away such that the clypeal sclerites form a floor to the head capsule in the anterior part of the buccal cavity and the labrum rests up against them with its tip pointing forwards and surrounded by the fleshy lobes at the end of the labial complex. The main labial sclerite, the *premental sclerite*, is then the plate seen bulging from the buccal cavity when the head is viewed from beneath.

There is no obvious sexual dimorphism in the structure of syrphid mouthparts. There is no external indication of mandibular sclerites in any of the genera examined during preparation of the present text.

Apart from in *Microdon*, two clypeal sclerites are present in Syrphidae: A *postclypeus*, articulating on its proximal margin with the anterior edge of the buccal cavity, and a more distal *anteclypeus*. The proximal edge of the anteclypeus articulates with the anterior edge of the postclypeus. The distal margin of the anteclypeus is deeply concave, its lateral arms passing forwards to articulate with the base of the labrum but visible externally only as narrow sclerotised strips (fig. 14). A solitary clypeal sclerite is present in *Microdon*, bearing a close resemblance to the anteclypeus of other Syrphidae (fig. 15).

The labrum is a heavily sclerotised, highly polished plate, in external appearance reminiscent of an upturned canoe. In genera such as *Rhingia*, with mouthparts adapted to nectar extraction from flowers with a deep corolla, the labrum is greatly elongate (fig. 16).

Roofed by the labrum, the food-channel is floored by the hypopharynx, a sclerotised, stylet-

like, concave sclerite, which projects forwards as far as the tip of the labrum. The pair of maxillary sclerites, with their unsegmented *palps*, lie in the membrane lateral to the sclerites of the food channel. Each maxillary sclerite is continuous internally with a sclerotised rod interpreted as the *stipes*, which passes back into the head capsule. In most genera the maxillary sclerites sweep down from their lateral position towards the mid-line, sheathing the hypopharynx ventro-laterally. The maxillary palps, conversely, sweep upwards, hugging the outer surface of the labrum so that distally they come to lie side by side along its dorsal surface. In some genera, e.g. *Merodon*, the maxillary palps are quite strongly sclerotised, but in the most cases they are membranous.

The identity of the maxillary sclerites, here termed the *maxillae*, remains an unresolved problem: See Matsuda (1965). Currently, they are most often regarded as the lacinia (e.g. in McAlpine, 1981). *Microdon* is exceptional among Syrphidae in possessing short, flange-like maxillary sclerites, orientated transversely rather than longitudinally. Also, the maxillary palps are rudimentary in *Microdon* (fig. 15).

The most complex and varied structure of the syrphid mouthparts is the labium and its appendages. Matsuda (1965) summarises the information available on the origin of dipteran labial structures. Essentially, of the two vertical labial sclerites the more basal, the postmentum, is absent. The other, the prementum, has become partly desclerotised but gave rise to the large external, ventral plate of the Syrphid labial complex (figs. 14–16) termed here the *premental sclerite*. The membranous lobes lying distal to the premental sclerite, collectively known as the *labellum*, are apparently derived from the original labial palps. The terminal lobes of the original prementum (glossae and paraglossae, together known as the ligula) have been lost. The partly membranous prementum containing the premental sclerite has become weakly resclerotised on its upper surface, producing a secondary sclerite (see fig. 16) known as the *hypoglossa* (usually hidden from sight when the mouthparts are examined in side view).

Within the labellum, the original two-segmented form of the labial palps has been modified but is evidenced from the position of largely internal strengthening rods, the *furca* and *epifuraca* (see Schiemenz, l.c.). In different Syrphids the labellar lobes exhibit a range of variation from the voluminous, convoluted, membranous flaps exhibited by *Syrphus* (fig. 14) to narrow, tongue-

like strips with strongly sclerotised tips such as are found in *Rhingia* (fig. 16).

In the literature reference is frequently made to regions of the proboscis called the *rostrum* and *haustellum*. The rostrum is the largely membranous basal section of the proboscis, as far as the base of the labrum and labium. The haustellum is then the most distal portion containing the mouthparts proper and including the labelum.

### The cervical region

In Diptera, the cervical region or cervix, is largely impacted onto the front face of the thorax. Its structures comprise three pairs of *cervical sclerites* (or *cervicalia*) and the *cervical organ* complex (figs. 17–19, 21). The main feature of the cervical region is the pair of *lateral cervical sclerites*. These flank the cervical cavity, along their outer edges articulating internally with prothoracic elements. Ventrally, the lateral cervical sclerites meet in the mid-line over the membranous pocket containing the cervical organ. Dorsally, arms from the lateral cervical sclerites twist forwards, flanking the lower edge of the cervical canal and articulating at their tips with the cervical condyles on the back of the head. Resting alongside the tips of the lateral cervical sclerites is the pair of small, dorsal or *anterior cervical sclerites*.

In the cervical membrane along the lower edge of the main body of the lateral cervical sclerites is found the pair of *posterior cervical sclerites*. In Syrphidae these are rather variable in appearance and in degree of sclerotisation. At their outer ends the posterior cervical sclerites appear to fuse with the prothoracic episterna. Their inner ends bear sclerotised outgrowths, as in *Syrphus* (fig. 21).

According to Matsuda (1970), in Diptera the lateral cervical sclerites are derived from pleural elements of the prothorax but the other cervical sclerites are secondary sclerotisations. The lateral cervical sclerites would most logically articulate laterally with propleural elements, and since the anterpronotum and proepisternum are indistinguishably fused somewhere in the region of the point of articulation of the lateral cervical sclerites, the position of that articulation has been used by some authors as an indication of the dorsal extent of the proepisterna. However, Matsuda (l.c.) has reduced the value of this argument by suggesting that in *Tabanus* the lateral cervical sclerites probably articulate with elements of the anterpronotum.

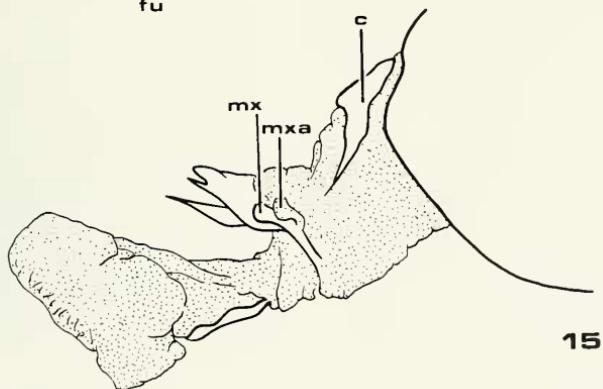
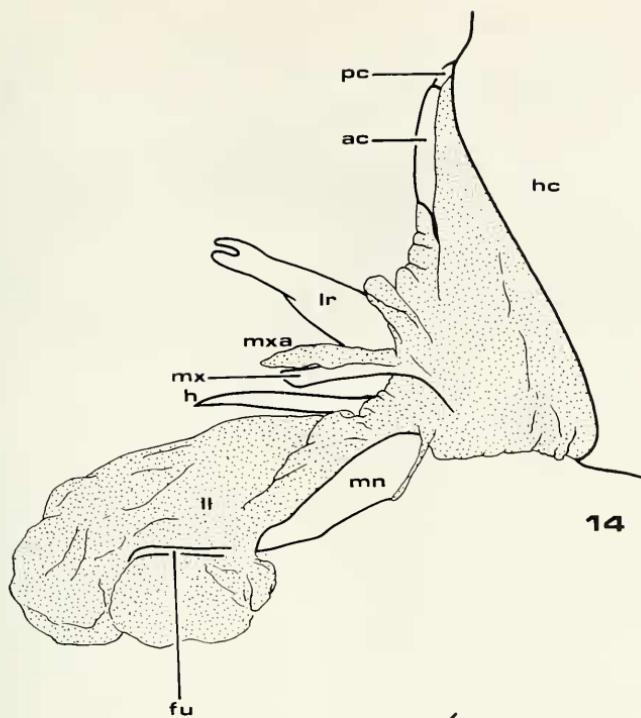


Fig. 14, *Syrphus ribesii*, mouthparts, lateral view. Fig. 15, *Microdon mutabilis*, mouthparts, lateral view.

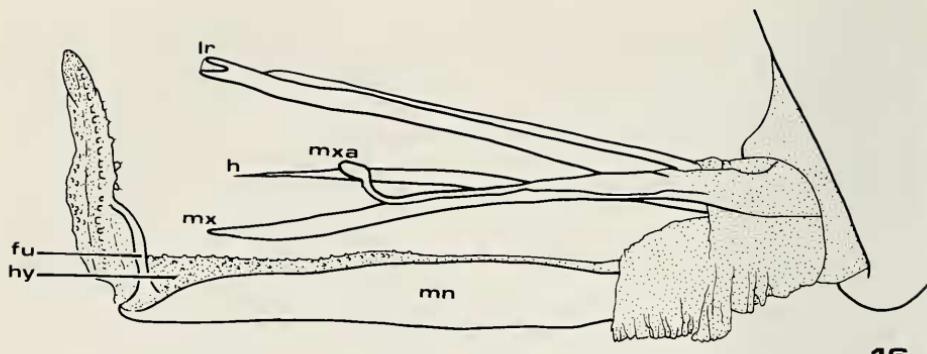


Fig. 16, *Rhingia campestris*, mouthparts, lateral view.

The cervical organ complex has received scant attention in Diptera, being entirely ignored in reviews of Dipteran morphology such as those conducted by Matsuda (1970), Bitsch & Matsuda (1973) and McAlpine (1981). The only published review of its structure in Diptera is that incorporated into Speight (1969). Among Syrphidae, the cervical organ is rather varied in its detailed structure, but is essentially a sensilla-bearing plate, termed the *sellula*, lying across the mid-line in a membranous pocket beneath the postero-median wings of the lateral cervical sclerites. The sensilla are directed upwards and slightly outwards so that their tips touch the underside of the postero-median wings of the lateral cervical sclerites. The sellula extends posteriorly in the mid-line as a sclerotised bar in the surface of the cervical membrane, where it articulates with, or is fused to, a median sclerite which some authors have identified as the presterum of the prothorax. Matsuda (l.c.), however, argues that this latter plate is more likely a secondary sclerotisation of the cervical region and should be regarded as a cervical sclerite. Here, because of its evident involvement in the functions of the cervical organ and its debateable origin, this plate is simply called the *postsellula*. In many genera, (e.g. *Syrphus*), at some point along its length the sellula expands laterally into a trapezoid, bearing at its lateral extremities a pair of sclerotised tubercles (fig. 21).

#### THE THORAX

Even a small amount of original research on muscle origins would probably produce dramatic

results in deciding correct designations for thoracic sclerites, since the number of Dipteran species whose thoracic musculature has been comprehensively investigated can almost be counted on the fingers of one hand. The only syrphid whose thoracic musculature has been reported on is *Eristalinus megacephalus* Rossi (as *Lathyrophthalmus obscuritarsis*), in Maki (1948). The degree of confusion existing at present can be adduced from a comparison between the terminologies employed for the Dipteran thoracic sclerites by Crampton (1942) and Matsuda (1970): hardly a single part of the thorax is given the same name in the two texts. In the present account an attempt has been made to follow the terminology employed by Matsuda (l.c.), with certain modifications based on McAlpine (1981). Unfortunately, Matsuda's text is based largely on a comparison between certain Tipulids, *Tabanus* and a Nycteribiid, augmented by occasional observations on *Drosophila*, and syrphid thoracic morphology presents features departing significantly from what has been observed in these other flies.

#### Prothorax

The most anterior of the three thoracic segments, the prothorax, is in Diptera an insignificant and incompletely delimited component of the front end of the thorax, overhung by part of the mesonotum. The prothoracic tergum, the pronotum, occurs externally as three sclerites, the *antepronotum* and the paired *postpronotal sclerites*. In Syrphidae, the antepronotum is dorsally reduced to a narrow semi-circular plate, deeply notched in the mid-line, arching round the

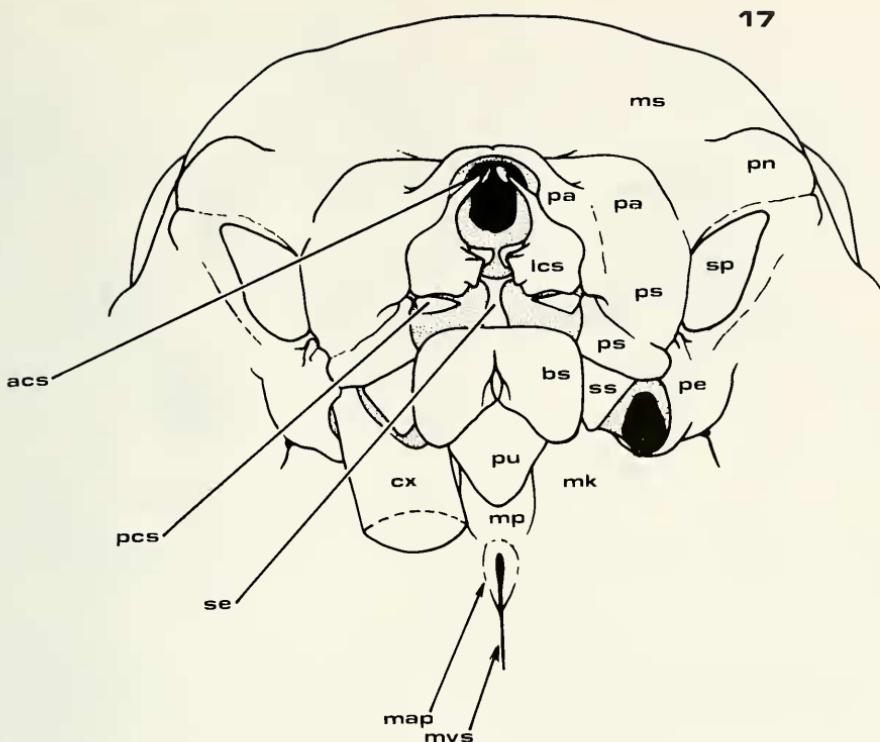


Fig. 17, *Eristalis tenax*, prothoracic region, anteroventral view.

upper edge of the cervical membrane. Laterally it widens out, passing ventrally to fuse indistinguishably with the prothoracic episterna. Posteriorly, in the mid-line, the antepronotum dips down into the deep, pit-like *antecostal suture* (fig. 20), from which the first thoracic phragma is invaginated. More laterally, the posterior edge of the antepronotum abuts onto the postpronotum, a junction marked by a complete suture in most Syrphidae, e.g. *Syrphus* (fig. 18).

The postpronotum is represented externally by the pair of sclerites forming at least the major part of the prominent humeral calli of taxonomists. Unless the antecostal suture occurs between antepronotum and postpronotum in Syrphidae, rather than between post-pronotum and meso-notal acrotergite as is generally supposed, the lateral elements of the postpronota are not externally connected with each other in these flies. Instead, the postpronotal sclerites appear to dip into the antecostal suture at its outer ends. In

the absence of information to the contrary, the suture curving up, over the humeral calli posteriorly, from the antero-dorsal edge of the prothoracic spiracle, is here taken to delimit the junction between postpronotum and mesonotal elements. This suture curves round towards the antecostal suture but then usually fades out, so that postpronotum and mesonotum are incompletely demarcated from each other.

The propleura comprise a *proepisternum* and a *proepimeron*. The proepisternum (propleuron of taxonomists) is fused anterodorsally with the antepronotum and anteroventrally with the posterior cervical sclerites. Some authors (e.g. Thompson, 1972) have recognised anepisternum and katepisternum in the proepisternum, but on what basis is unclear. The position of the anterior edge of the proepimeron can be detected by the line of the propleural suture, which divides proepisternum from proepimeron and runs from the rim of the fore coxal cavity to the prothoracic

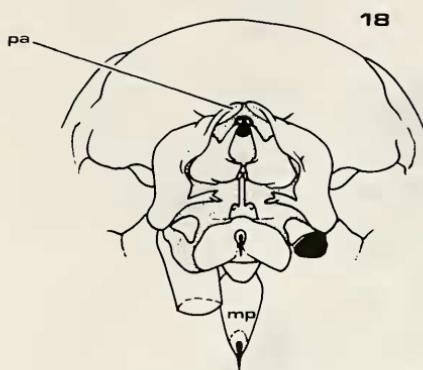
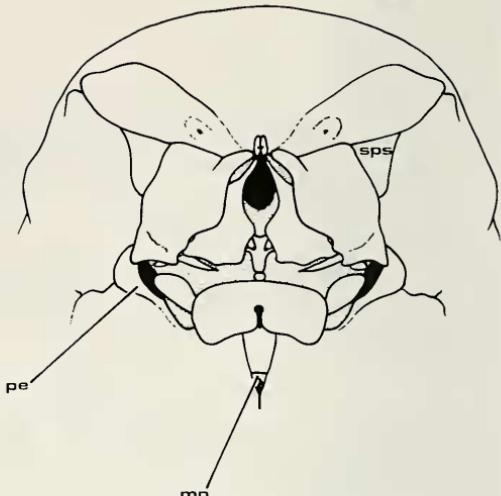


Fig. 18, *Syrphus ribesii*, prothoracic region, anteroventral view. Fig. 19, *Microdon mutabilis*, prothoracic region, anteroventral view.

spiracle. In *Microdon* (fig. 19) the posterior edge of the proepimeron appears to be marked by a suture for part of its length, but it is otherwise not differentiated from mesopleural elements.

Anteroventrally, a projection of the proepisternum articulates with or fuses to the posterior cervical sclerites. This projection is to a variable extent marked off from the main body of the proepisternum by a suture and may or may not represent the remains of a propleural precoxal — it is given no separate designation in this account. Another sclerite which could be interpreted as either the propleural precoxale or a trochantin lies free in the cervical membrane along the anterior rim of the coxal cavity, between proepisternum and probasisternum. This sclerite is often poorly sclerotised and may be absent. Here it is regarded as of secondary origin and labelled simply as a secondary sclerite (figs. 17—19).

The sternum of the prothorax is represented externally by a *basisternum* and a *furcasternum*. The "presternum" of some authors is discussed in that section of the present account dealing with the cervical region. The basisternum (prosternum of taxonomists) is a large median plate interposed between the cavities of the fore coxae, carrying a pronounced median sulcus, from which is invaginated the basisternal carina. In

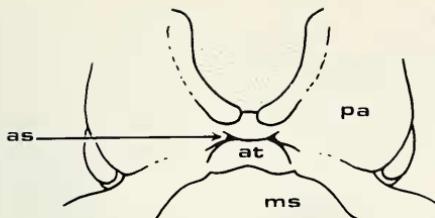


Syrphidae the probasisternum is clearly differentiated along all its margins. It does not seem to join with propleural elements to form a precoxal bridge in any members of this fly family. On its anterior margin the probasisternum is in the mid-line contiguous with the sella or postsella of the cervical organ.

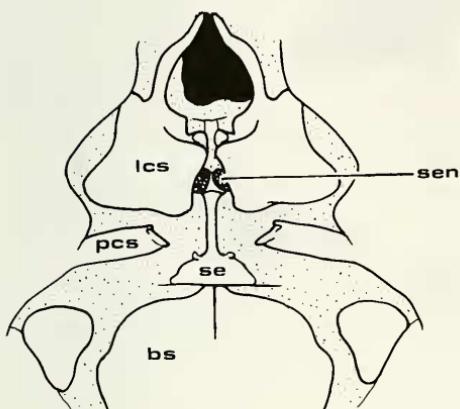
The profurcasternum is in syrphids a median, ventral, triangular sclerite (figs. 17—19), joined anteriorly to the probasisternum, from which it is delimited by a complex suture. It meets the mesothoracic presternum posteriorly, anterior to the point at which the latter plate disappears into the mid-ventral thoracic suture. In its anterior angles the profurcasternum bears the furcal pits from which the furcal arms are invaginated.

#### Mesothorax: mesonotum

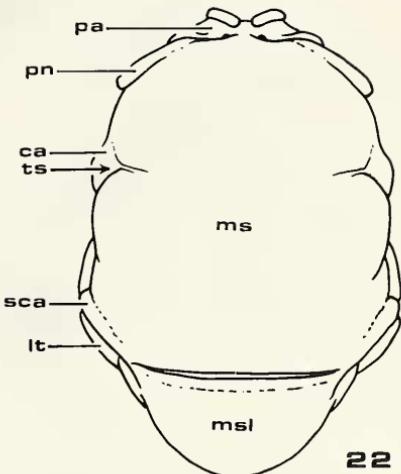
In Diptera the mesothorax is greatly expanded and makes up the main bulk of the thoracic surface. This expansion is presumed to be due to the need to accommodate the flight musculature associated with the fore wings, which are attached on this thoracic segment between pleural and tergal elements. Coincident with the expansion of the musculature has been differentiation of a complex endoskeleton, the *mesosternal apophysis*.



20



21



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Fig. 20, *M. mutabilis*, prothoracic region, anterodorsal view. Figs. 21, 22, *Syrphus ribesii*, cervical region, anteroventral view (21) and thorax, dorsal view (22).

*sis*, for muscle attachment. In most Diptera — including Syrphidae — almost the entire mesothoracic sternal region is invaginated into the thorax as the mesosternal apophysis.

Viewed from above, the Syrphid thorax is nearly all of mesonotal origin (fig. 22). The mesothoracic notum, or mesonotum, is made up of five sclerites. The most anterior of these is the *acrotergite*, possibly visible on the antero-dorsal face of the thorax in *Microdon* (fig. 20), but otherwise seemingly not discernible in Syrphidae. The acrotergite is followed by the *prescutum*, which is reduced to a pair of lateral, unconnected strips, running along the edge of the mesonotum from just above the prothoracic spiracle to as far as the transverse sulcus of the mesoscutum. These *prescutal strips* are usually just visible when the thorax is examined from the side (fig. 23), but are so reduced in *Microdon* as

to be unrecognisable without first partially desclerotising the specimen. Even then they cannot be seen in side view, being concealed beneath the lateral edge of the mesoscutum.

The *mesoscutum*, generally known among taxonomists as the mesonotum, is the main mesonotal sclerite. Although its anterior and posterior sutures are incomplete, it is well differentiated laterally and includes the morphological features known taxonomically as the "notopleural area" (or "presutural area") and the "post-alar calli". The confusing term notopleural area (and associated terms notopleural depression and notopleural callus) is not used here, since the part of the thorax to which it refers is in origin mesonotal, not mesopleural. The alternative term of *presutural area* (and associated terms *presutural depression* and *presutural calli*) is used in its place. The mesoscutum carries a shallow trans-

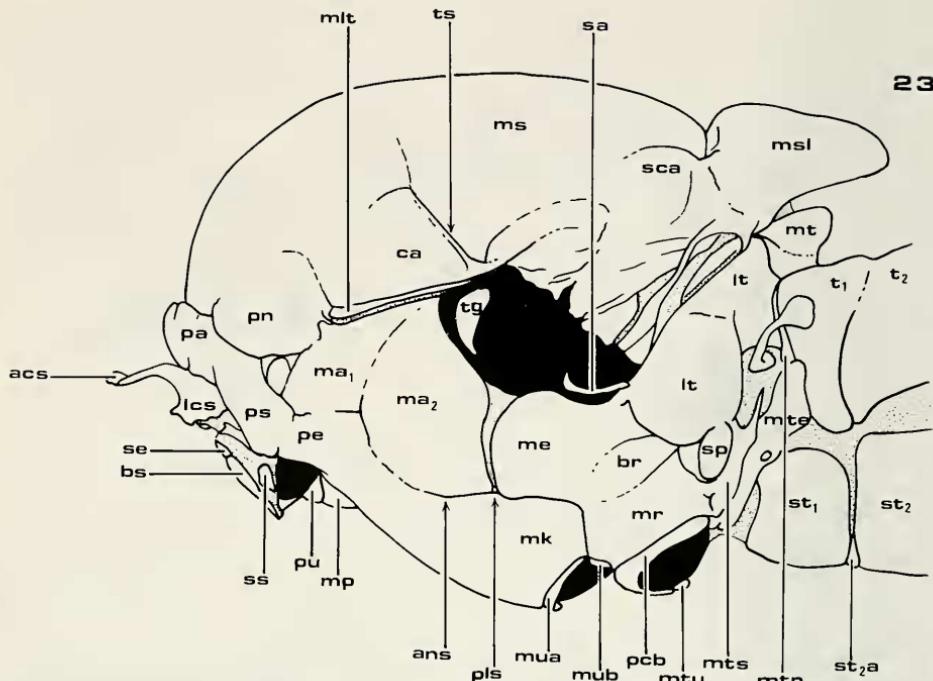


Fig. 23, *S. ribesii*, thorax, lateral view, left side.

verse gulley, just anterior to the wing base. A similar feature occurs in many different Diptera and has been given various names: transverse suture, lateral parapsidal suture, scutal suture, transcutal suture. Since, according to Matsuda (1.c.), this feature is intra-scutal and thus does not mark a joint between sclerites, it should ideally be termed a sulcus, following Snodgrass (1960). Diptera may carry up to three distinct transverse sulci on the mesoscutum, but Syrphidae luckily only exhibit one, so whatever its homologies (see McAlpine, 1981), it can conveniently be called "the transverse sulcus," which is the term used for it here. At the outer ends of the transverse sulcus of the mesoscutum, *Microdon* possesses a pair of shelf-like, semi-circular, sclerotised outgrowths of the mesoscutum, which do not seem to have an equivalent in other Syrphids. The prescutal strips are beneath these mesoscutal flanges.

Posteriorly, the suture marking the mesoscutal junction with the succeeding mesonotal sclerite, the scutellum, has been lost. The very deep and well-marked trans-scutellar sulcus is located

within the mass of the original mesoscutellum: (see Matsuda, 1.c.), so that some indeterminate portion of the hind part of the "mesonotum" of taxonomists is scutellar in origin. In syrphids the hind part of the mesoscutum differentiated by the transscutellar sulcus protrudes from the posterior end of the dorsal thoracic surface as a well-defined semi-circular lobe, generally called the scutellum by taxonomists. Here, this feature is called the *scutellar lobe*. In some genera its outer (postero-dorsal) edge is tuberculate or crenulate. Ventral to the scutellar lobe is the median plate of the most posterior of the mesonotal elements, the *mesopostnotum* (also known as the mediotergite, or subscutellum or postscutellum), flanked by its two lateral sclerites (figs. 23, 24). These are the *lateral post-nota* of the mesonotum, also known as the laterotergites (or pleurotergites). Some authorities, e.g. Colless & McAlpine (1970), currently regard these postnotal sclerites as derived from the acrotergite originally interposed between mesonotal and metanotal elements, rather than from the mesonotum. The *median postnotum* is normally a convex

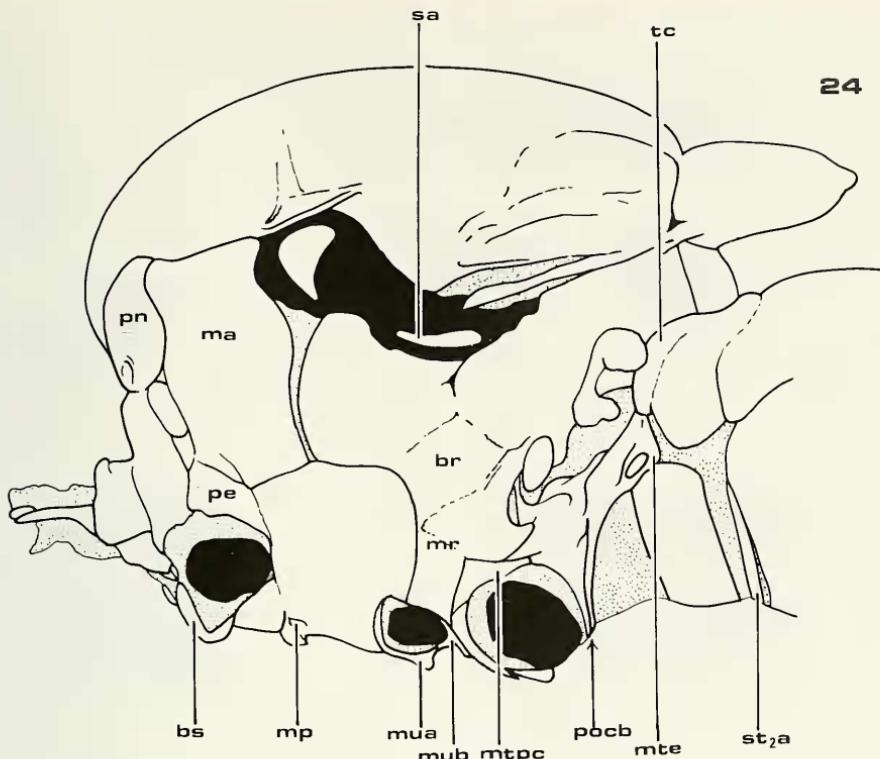


Fig. 24, *Microdon mutabilis*, thorax, lateral view, left side.

plate in *Syrphus* and its relatives (fig. 23), pushing out into a distinct lobe. But in *Microdon* (fig. 24) it is unusually flat. The lateral post-nota form shallow calli just dorsal to the metathoracic spiracles, but continue towards the mid-line beyond these calli to a point where an unobtrusive suture marks their junction with the median postnotum. Antero-dorsally, the lateral postnota border the posterior part of the wing-base complex of axillary sclerites. Postero-ventrally, the lateral post-nota border the similar, but physically much smaller, complex of sclerites round the base of the haltere. The massive second thoracic phragma attaches directly to the hind margin of the median postnotum and passes down internally to form the sclerotised hind wall of the functional thorax. The second phragma stops just short of the floor of the thorax, immediately above the membranous strip between hind coxae and first abdominal sternite that acts as a thoracic/abdominal flexion joint. Certain small,

detached sclerites located in the axillary complex are believed to be derived from the mesonotum. These include the *tegula*, *humeral plate*, 4th *axillary sclerite*, and *subalare*. They are dealt with in that portion of the present text concerned with the wings.

#### Mesothorax: mesopleura

The pleural sclerites of the second thoracic segment exhibits in Diptera a bewildering array of bumps, hollows and grooves, some of which represent primary subdivisions of the pleura and most of which have been employed as taxonomic characters at some time or another. In Syrphidae, most of the side of the thorax is mesopleural in origin. The largest recognisable entity is the *meseipisternum*. The anterior margin of this sclerite is marked by the posterior edge of the prothoracic spiracle, from which an incomplete suture extends towards the fore coxae, the me-

sepisternum being fused with propleural elements ventrally. In the mid-line ventrally, the mesepisterna meet along the line of the mid-ventral suture, which terminates anteriorly in the mesofurcal pit. Posteriorly, the upper part of the edge of the mesepisternum is marked by the vertical membranous strip of the pleural suture. The pleural suture continues downwards as a well-marked groove, taking a zig-zag course toward the mid-coxae. The lowest (third) section of the suture is unusually complete in Syrphidae, being especially well-marked in *Microdon* (fig. 24). Dorsally, the margin of the mesepisternum is indicated by the suture delimiting mesonotal elements and by the membranous area round the wing-base containing the axillary sclerites (some of which are mesepisternal in origin).

Within the mesepisternum, various subdivisions may be recognised. From the ventral end of the upper (first) section of the pleural suture the incomplete anapleural suture proceeds forwards, dividing the mesepisternum into a dorsal *anepisternum* (the "mesopleuron" of taxonomists) and a ventral *katepisternum* (see McAlpine, 1981, for reasons why the ventral area of the mesepisternum delimited by the anapleural suture should be regarded as *kat*-episternum rather than *pre*-episternum). The katepisternum is the "sternopleuron" of taxonomists. The anepisternum may be further differentiated into an antero-dorsal flat area (the "anterior depressed portion of the mesopleura" of Coe, 1953, and the "anterior flat portion of mesopleuron" of Vockeroth, 1969), and a shallow more posterior callus (fig. 23). These fields of the anepisternum are frequently mentioned independently in taxonomic texts but do not seem to have been named, other than by Speight (1980), where they were referred to as mesopleurite 1 and mesopleurite 2. They would be better called *anepisternite 1* and *anepisternite 2*, and these terms have been used to denote them here.

The *mesothoracic epimeron* is clearly delimited anteriorly by the pleural suture. Posteriorly its edge is marked by the suture between it and the lateral postnotum of the mesonotum. Ventrally, it is fused with a plate regarded as the mesothoracic meron, to produce a composite sclerite known as the *meropleurite*. In Syrphidae the mesepimeron and the meropleurite are hardly differentiated from each other by sutures. The upper part of the mesepimeron corresponds more or less with the "pteropleuron" of taxonomists. It is flat above but exhibits a transverse callus below, just above where its junction with

the meropleurite is probably located. The flat part is regarded by McAlpine (1981) as the mesepimeral anepimeron and the callus as the mesepimeral katepimeron. The callus is of taxonomic significance and by taxonomists has been called the *barrette*, a term used for it here. The meropleurite corresponds roughly with the "hypopleuron" of taxonomists, though the term hypopleuron has been applied in such a way that it also includes metapleural elements.

#### Mesothorax: mesosternum

Mesosternal elements are surprisingly well represented externally in Syrphidae — in Schizophora the mesosternum is, almost in its entirety, invaginated into the thorax. In the three syrphids illustrated here (figs. 26—28) the mesosternal *presternum* is clearly differentiated from the preceding prothoracic furcasternum and invaginated posteriorly into the mesofurcal pit at the beginning of the mid-ventral thoracic suture. Laterally, the meso-presternum meets mesepisternal elements, from which it is less clearly separated. The two wings of the anterior *mesosternal furcasternum* each occur externally as a narrow strip along the anterior rim of the mesocoxal cavities, dipping down into the mid-line to reappear posteriorly as the ventral *coaxal condyles*, articulating with the median mesocoxite (figs. 26—28). The *posterior mesosternal furcasterna* make a hind rim to the mid coxae. These external furcasternal elements are continuous internally with the massive mesofurca, without indications of sutures interposed, thus reducing the probability that they might be better interpreted as some vestige of a mesopleural trochantin.

#### Metathorax

The metathorax is probably the least studied region of the external anatomy of Diptera and apart from the remarkable paper of Young (1921) has been largely ignored in the literature.

Whatever elements may have once been present in the *metanotum*, it is represented in Syrphidae solely by a narrow hoop-like sclerite evanescent medially in some genera, hugging the antero-dorsal face of the abdomen but invaginated along its anterior edge into the suture marking externally the position of the second thoracic phragma (figs. 41—43). Due to its location it is often only visible at its dorso-lateral corners, when the abdomen is viewed from above. In side view it can be quite concealed on the front of the abdomen, by a forward bulge of abdominal tergite 1, as in *Microdon* (fig. 24). In

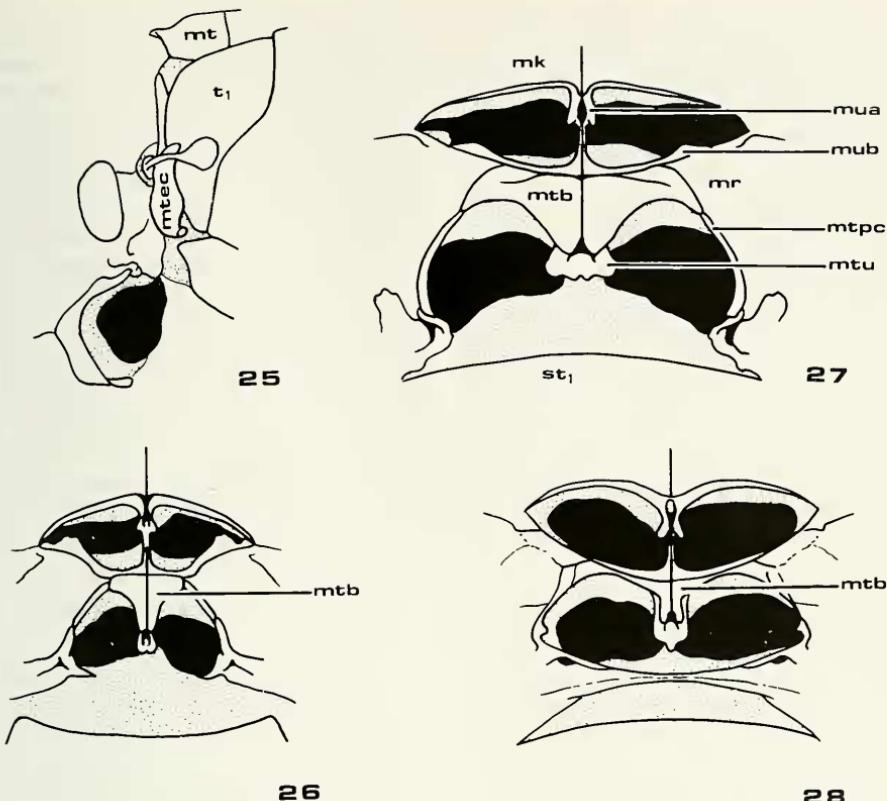


Fig. 25, *Eristalis tenax*, thorax, region surrounding the haltere, lateral view, left side. Fig. 26, *Syrphus ribesii*, meso and metathoracic sterna, ventral view. Fig. 27, *Eristalis tenax*, meso and meta thoracic sterna, ventral view. Fig. 28, *Microdon mutabilis*, meso and methatoracic sterna, ventral view.

*Syrphus* (fig. 41) the metanotum bears a distinct transverse groove which could represent the suture between two of the original metanotal sclerites. Equally, this groove might be a secondary feature. No attempt has been made to identify subdivisions of the metanotum. Laterally, the metanotum fuses with metapleural elements, the junction being in some instances, e.g. *Syrphus*, distinctly marked.

The metapleura comprise an *episternum*, an *epimeron* and a *precoxale*. The met-episternum is imperfectly demarcated from both mesothoracic meropleurite anteriorly and metathoracic epimeron posteriorly and can only be detected clearly immediately posterior and ventral to the metathoracic spiracle. In some genera the metepisternum appears to contact the lateral postno-

tum of the mesonotum behind the metathoracic spiracle (see *Eristalis*, fig. 25), but in others membrane of the haltere axillary complex intervenes (see *Microdon*, fig. 24). Ventrally, the metepisternum may, in combination with the metepimeron, form a postmetacoxal bridge (fig. 28).

The metepimeron, as interpreted here, exhibits some unlikely characteristics. That it is incompletely delimited from the metepisternum has already been mentioned. Postero-ventrally, the metepisternum is bordered by membrane interposed between it and abdominal sternite 1. In forms lacking a postcoxal bridge this membrane is continuous with that of the meta-coxal cavities. In some syrphids, the metepimeron bulges postero-dorsally into a distinct callus on the front margin of the first abdominal tergite (fig. 25),

from which it is separated by reflexed membrane. This metepimeral callus is frequently visible from above as an angular projection on the outer, anterior corner of tergite 1, and is especially visible in *Neoscia* (fig. 44) where it is developed into a massive spine — illustrated in Stackelberg (1965) as apparently part of abdominal sternite 1. The metepimeron frequently encloses the first abdominal spiracle at its lower edge (figs. 23–25). In *Microdon* and *Ceriana* this callus is lacking, but the first abdominal spiracle is still enclosed by the metepimeron in European species of these genera. In *Eristalis*, the first abdominal spiracle occurs partly in the metepimeron and partly in the adjacent abdominal membrane. Zumpt & Heinz (1949) regarded the metepimeral callus of *E. tenax* as either a secondary sclerite or a part of abdominal tergite 1.

The metacoxal precoxale is a narrow sclerotised strip clearly differentiated round the lateral rim of the metacoxal cavity. At its posterior end it reaches the lateral condyle of the metacoxa. Anteriorly, it joins with the metabasisternum in most hoverflies, to form a composite sclerite making a precoxal bridge round the metacoxae. It retains its identity independent of the metabasisternum in *Melanostoma* and *Sericomyia*.

The principal metasternal sclerite is the metabasisternum, a mid-ventral plate located between and anterior to the hind coxae. It is deeply grooved in the mid-line and frequently fused with the metaprecoxale laterally, as described above. The premetacoxal bridge thus developed is frequently called the "metasternum". Its particular make-up requires that it be given some morphological appellation such as metabasisterno-precoxite — not a term likely to be met with general approval! For want of a more appropriate alternative this composite structure is referred to here as the *premetacoxite*. With the postmetacoxal bridge, the premetacoxal bridge forms in some syrphids, e.g. *Sphegina*, a pronounced conical bump protruding postero-ventrally from the underside of the thorax.

The other external sclerite of the metasternum is the vestigial furcasternum, projecting from within the thorax to form the *ventral meta-coxal condyles*, to either side of the mid-line just posterior to the tip of the metabasisternum.

## WINGS

In Diptera only the fore wings (hereafter referred to as "the wings") remain as organs of flight, the hind wings being modified into gyro-

copic organs known as the halteres. As described in preceding pages, the wings and the halteres are located on the side of the thorax between tergal and pleural elements. Externally, the junction between wing and thorax is marked by a cluster of axillary sclerites and associated membrane, which may be referred to as the axillary complex. The haltere base has a corresponding axillary complex.

The wing itself is a largely transparent sheet of membrane, traversed by a series of sclerotised bars, the wing-veins, radiating from the wing-base. In syrphids there are six major wing veins. Those radiating into the middle area of the wing branch one or more times before reaching the wing margin. Occasional cross-members are also present, termed cross-veins. The wing-membrane is in some genera banded or blotched with brownish pigment and may be all or in part covered by microtrichia. The most posterior fields of the wing-membrane are largely separated from the main body of the wing, going to form the *alula* and, folded beneath the wing-base, the *calypters* (fig. 31).

Attempts have been made by morphologists and taxonomists alike to homologise the main fields of the wing-membrane and the main wing-veins, throughout the various Orders of insects. The wing-vein notations resulting have been largely incompatible, but nonetheless many authors have adopted hybrid wing-vein terminologies based partly on one theory and partly on another. Wootton (1979) provides an able review of the present chaos, which affects syrphid wing-venation notation along with that of other Diptera. Goffe (1947) attempted to derive a stable system for naming syrphid wing-veins, but unfortunately the notation he proposed is a confusing hybrid. Alternative notations, differing from one another to a greater or lesser extent, can be found in Coe (1953), Colles & McAlpine (1970), McAlpine (1981), Matsuda (1970), and Seguy (1959, 1961), etc. In the present account, Colless & McAlpine (1970) are followed, with modifications suggested by Wootton (1979).

The nomenclature of the three most anterior longitudinal wing-veins, named here the *Costa*, *Subcosta* and *Radius*, is reasonably stable in Diptera. However, the next vein, the *Radial Sector*, has anomalously usually been labelled as though its branches were branches of the Radial. That convention is not adopted here, following Wootton's recommendation. The following three veins, here named the *Median*, the *Anterior Cubitus* and the *Posterior Cubitus* have been much

confused, the appropriate designations for distal branches which could be derived from either the Median or the Anterior Cubitus (or represent cross-veins — see below) remaining today almost a matter of personal opinion. The vein regarded here at the Posterior Cubitus has been omitted from illustrations of syrphid wing-venation by some authors, e.g. Oldroyd (1970). The *First Anal* vein as recognised here is labelled as such in most recent literature, but Wootton (1979) suggests the cubito-anal area of the wing may well have been misinterpreted by dipterists, and the true anal veins may well be confined to the alula in Diptera. Elucidation of that problem awaits further work, as Wootton (1.c.) himself says, so the more traditional approach to the identity of the First Anal has been adopted in the present text.

The more basal cross-veins of the syrphid wing have generally received the same designations, but there are differences of opinion as to which of the more distal cross-veins are actually transversely deflected branches of longitudinal veins. Thus the vein labelled here as an anterior branch (M.1) of the Median, has been called the "upper marginal cross-vein" and the vein labelled *marginal cross-vein* has often been regarded as a branch of the Anterior Cubitus.

The areas of membrane entirely enclosed by wing-veins comprise the "cells" of the wing. One approach to naming wing-cells is to number them from the anterior margin of the wing backwards. An alternative approach is to designate them according to their position on the general wing-surface, a system which gives rise to costal cells, basal cells, marginal cells, etc. This system, as laid out in Oldroyd (1970) is employed in the present account (fig. 29). Neither system is very satisfactory because of the problems of homology of wing-cells in fly families — like the Syrphidae — in which few wing-cells are present.

A venational characteristic of Syrphidae, mentioned almost universally in the literature, is the *vena spuria*. This secondary strengthening of the wing membrane lies between the Radial Sector and Median veins and is more or less parallel with the latter. Almost invariably it crosses the *radio-median cross-vein* into the *posterior cell*, but most of its length is found in the *first basal cell* where it may proceed almost as far as that cell's inner end. Although popularly regarded as one of the most characteristic features of the Syrphidae, the *vena spuria* is entirely absent in some species, for example, *Syritta flaviventris*.

According to Wootton (1.c.), in Diptera the

area of the wing posterior to the 1st Anal vein and including the *alula* is homologous with the *claval field* recognised in other insects. The *jugal field* is then represented by the *calypters*. The cleft between the alula and the main body of the wing is generally termed the *axillary incision*. The alula is a simple membranous flap, its only venation a vein-stub at its postero-basal corner. The calypters hinge onto the base of the wing via the 3rd and 4th axillary sclerites (fig. 31). The upper calypter is folded over the lower when the wing is at rest, but when the wing is stretched out, as in the illustration (fig. 31), their relation to the rest of the wing membrane can be better appreciated. The rim of each calypter is somewhat sclerotised and bears a thick fringe of long hairs.

The axillary complex of the Syrphid wing-base has not been thoroughly investigated in the compilation of this account. Suffice it to say that there are four principal *axillary sclerites* in Diptera. The 1st and 2nd have been tentatively identified in fig. 31, following Matsuda (1970). The 3rd and 4th are easier to distinguish. Axillary sclerites 1–3 represent detached basal parts of the wing-veins (Matsuda, 1.c.), while the 4th is supposedly mesonotal in origin. On the front margin of the wing, two basal sclerites may be distinguished, the *humeral plate*, and the *tegula*. These are apparently homologous with the sclerites of the same name found in other Orders and are seemingly of mesonotal origin. A detailed account of the Dipteron wing-base complex is given by McAlpine (1981).

A final important feature of the axillary complex is the *subalare*. Although located beneath the wing-base, according to Matsuda (1.c.) this sclerite is of mesonotal origin. In Syrphidae it carries the *plumule*, a feature unique to the family. The plumule is a membranous, finger-like appendage, thickly covered in long, fine, wavy hairs. It projects backwards from the posterior tip of the subalare and thus lies closely opposed to the underside of the lower calypter. It is an easily seen feature in all syrphids except *Neoascia* and *Microdontinae*, where it is rudimentary and represented only as a rather hairy tip to the subalare, and in *Ceriana/Sphiximorpha*, where it is not recognisable. In *Myathropa* it reaches an opposite extreme of development, the entire outer rim of the subalare giving off small, plumulate appendages.

According to Bonhag (1949) and Mickoleit (1962), who worked on *Tabanus* and *Tipula*, respectively, the haltere base possesses clustered

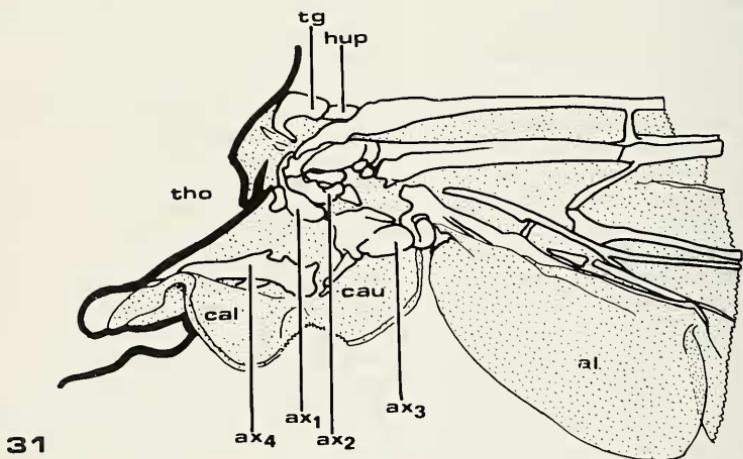
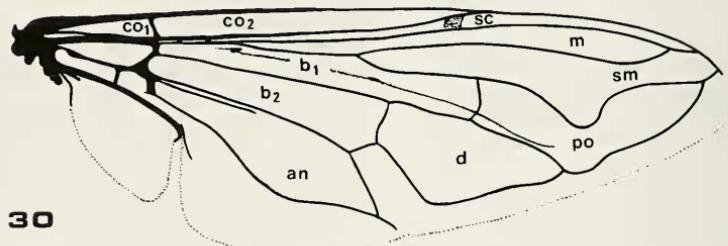
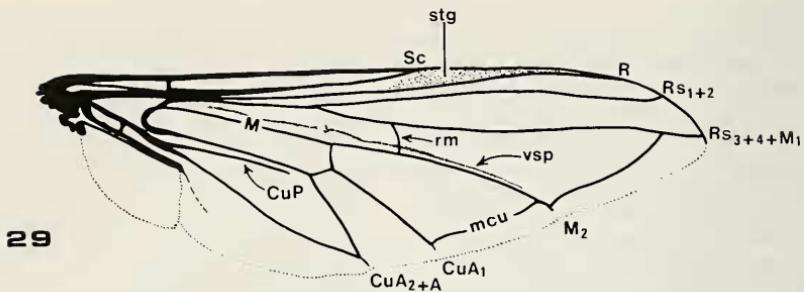


Fig. 29, *Syrphus ribesii*, right wing. Fig. 30, *Eristalis tenax*, right wing. Fig. 31, *Syrphus ribesii*, axillary region of right wing.

around it miniaturised versions of the axillary complex sclerites found round the base of the fore wings, but the haltere base sclerites do not seem to have been examined in any species of Syrphidae and they have not been investigated for the purposes of the present account. The haltere itself is a roughly dumbbell-shaped structure broadening rather abruptly at the distal end of its stalk into the head or knob and more gradually at its base.

### LEGS

The legs of syrphids comprise the following elements; *coxa*, *trochanter*, *femur*, *tibia*, five tarsal segments (or tarsomeres) and *pretarsus*, typified by the fore leg of *Syrphus* shown in fig. 34. The fore and hind coxae are single sclerites, fully mobile and articulated basally to the thorax, apically to the trochanter. The mid coxa, however, is made up of three separate sclerites or coxites (fig. 36). The *anterior mesocoxite* is fused to the thorax, but the *posterior* and *median mesocoxites* are mobile. The median mesocoxite articulates with the mesothoracic furcasternum via the coxal condyle and also with the other two mesocoxites. The posterior mesocoxite articulates with the anterior mesocoxite as well as with the median mesocoxite.

Almost universally in Syrphidae — *Microdon* representing the exception — there is a long, blade-like process projecting outwards from the antero-lateral end of the outer side of the posterior mesocoxite. This blade-like process, termed here the *trochanteral process of the posterior mesocoxite* (figs. 35, 36) fits into a shallow hollow on the surface of the mesotrochanter, when the leg is in certain positions.

In all three pairs of legs the segments from the trochanter outwards (inclusively) are all individual sclerites, essentially tubular and articulated to each other. Only the pretarsus is more complex. This, the terminal leg-joint, is attached within the concave end of the most distal (the fifth) tarsal segment. The pretarsus includes a central process terminating in a bristle-like or peg-like *empodium*, flanked by a pair of membranous pads known as the *pulvilliæ*, which are themselves attached to the central process via small sclerotised plates called the *auxilliae* (fig. 37). The lower surface of each pulvillus is in syrphids densely covered in short hairs. Above the pulvilliæ are found a pair of simple *claws*, which attach to a median apical projection of the 5th tarsal segment known as the *unguifer process*.

The first tarsal segment is usually referred to as the *basitarsus* or (confusingly) as the *metatarsus*. The undersides of the tarsal segments, in particular, carry arrangements of short, blunt bristles used in cleaning the body surface and the hind basitarsi have a ventral brush of close-packed bristly hairs used for this same purpose.

Although the number of leg segments remains the same throughout the family, in a significant number of genera one or more of the leg segments are modified in form, the modifications in nearly all cases being more pronounced in the males than in the females. In some genera, such as *Platycheirus*, in which the male fore tarsal segments are flattened and expanded laterally, the vast majority of species exhibit the same general type of modification. In others only single species may be affected — thus *Sphegina platyphira* males possess flattened tarsal segments reminiscent of those of species of *Platycheirus*, but the tarsi of other *Sphegina* species are unmodified. Almost any part of the leg may be affected by such modifications in Syrphidae, though usually segments of either fore or hind legs are involved. Rarely, as in *Neocnemodon latitarsis*, all three pairs of legs have some segments modified. In the male of *N. latitarsis* the fore basitarsi exhibit a large pit on one surface, the mid-tibiae are expanded into a leaf-like flange for about half their length and the trochanters of both hind and mid legs carry pronounced tines (fig. 39), as do the hind coxae. A frequent modification of the hind legs is for the hind femora to become bulbous and carry some arrangement of pegs and/or tubercles and for the hind tibiae to become angular and ridged (fig. 40).

### THE ABDOMEN

There is great sexual dimorphism in the form of the terminal segments (and occasionally in the form of some of the more anterior segments as well) of the syrphid abdomen, requiring that the male and female abdomen be given detailed consideration separately. In the male the abdomen is divided into two distinct sub-regions, a largely unmodified "preabdomen" and a highly modified "postabdomen". Equivalent terms are not used in relation to the female abdomen. Certain features of the abdomen common to both sexes may be considered at this juncture.

As viewed from above, the overall shape of the syrphid abdomen exhibits considerable variation. It may be conical, parallel-sided, ovate or petiolate. These shape differences are due largely to

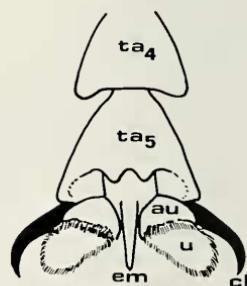
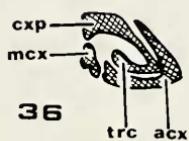
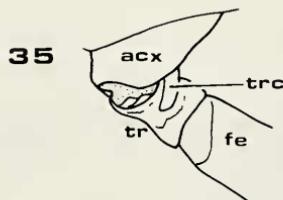
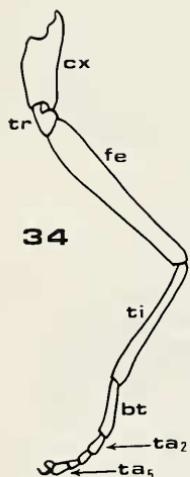
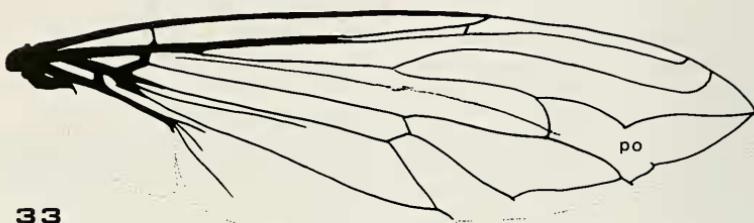
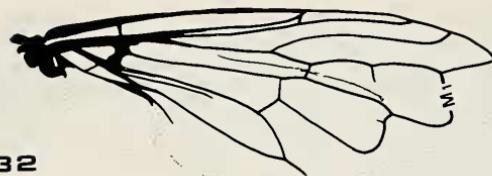


Fig. 32, *Microdon mutabilis*, right wing. Fig. 33 *Ceriana* sp., right wing. Figs. 34—36, *Syrphus ribesii*, left fore leg, anterior view (34), male, base of left mid leg, antero-lateral view (35) and diagrammatic representation of mid coxa to show inter-relation between the three meso-coxites. Fig. 37, *Microdon mutabilis*, pretarsus and last two tarsomeres of left hind leg, ventral view.

intergeneric differences in the shapes of the visible abdominal tergites, rather than to differences in the number or identity of the sclerites in view. The number of visible tergites is four or five in the male and generally five or six in the female.

The first abdominal tergite (t.1) is largely fused with the second (t.2) in Syrphidae, though the junction between the two sclerites is usually evident. The anterior margin of t.1 is frequently complex, since in most syrphids the flexion line between thorax and abdomen passes through it, as in *Eristalis* and *Syrphus* (fig. 41). In such cases there is a median area of t.1 which reaches forwards to the metanotum, flanked by narrower lateral areas of t.1 which do not reach the metanotum and are partly separated from the median area of t.1 by an incomplete, transverse membranous cleft. *Paragus* (fig. 42) is an exception. In this genus the anterior margin of t.1 is straight and membrane intervenes between it and the metanotum across its entire width, leaving the abdomen noticeable more capable of flexion than in most other genera. A prominent feature of certain genera, such as *Ceriana*, is a pair of antero-lateral calli on t.1, giving the impression that an extra sclerite is present on the front margin of the tergite (fig. 43).

Tergite 2 is a large sclerite with the joint between it and tergite 3 (t.3) usually clearly marked. The actual anterior margin of t.3 is concealed beneath the hind margin of t.2, the two tergites being joined to each other by folded membrane. This type of junction is common to succeeding tergites except (e.g. in *Microdon*) where two tergites are fused to each other: tergites 2 and 3 are fused in *Paragus*; tergites 3 and 4 are fused in *Microdon*. In *Triglyphaeus* tergite 3 is greatly expanded, occluding t.4 and t.5 from view.

With the exception of the first, the abdominal spiracles are always found in the membranous strip between tergites and sternites. The first abdominal spiracle is more often than not enclosed within the metathoracic epimeron which is (as described earlier) in part functionally a component of the abdomen, together with the metanotum. In *Microdon* it was only found possible to locate the 1st abdominal spiracle during the course of this study.

The abdominal sternites are generally rather poorly sclerotised rectangular sclerites with rounded corners, lying free in the membrane of the underside of the abdomen. The 1st abdominal sternite may be largely desclerotised and much reduced. The second abdominal sternite (st. 2) is

divided in two by a transverse membranous strip. The sclerotised anterior part of st. 2 then appears in some genera, e.g. *Microdon*, as a separate, narrow plate lying along the entire anterior edge of the main sclerite (fig. 48). In *Eristalis* and *Syrphus* (fig. 47) this anterior plate of sternite 2 is a lunulate piece confined to the middle half of the width of st. 2. In *Sphegina clunipes* (fig. 45) the two sclerotised parts of sternite 2 are separated from each other by an appreciable distance, though the intervening membranous section of the sternite evidently connects them to each other.

#### Male abdomen

In Diptera the male abdomen is regarded as comprising eleven segments (numbered from the thorax to the abdomen tip). In the Cyclorrhapha in general there is extensive modification of segments 6—10 in the male due to their incorporation into the copulatory apparatus. Segment 11 is rudimentary, represented only by the cerci (which flank the anus). The term "preabdomen" is used to denote the unmodified portion of the male abdomen and "postabdomen" to refer to the modified portion. Zumpf & Heinz (1949) have argued that the postabdomen commences with segment 5 in *Eristalis*, since its structure is also greatly modified by involvement in the copulatory apparatus. Thompson (1972) points out that defined in this fashion the preabdomen comprises but four segments throughout the Milesiinae, but is found in its more usual 5-segmented form throughout the Syrphinae. The sclerites of the male postabdomen have become markedly asymmetrical, associated with a twisting or torsion of the segments on the long axis of the abdomen and a progressive recurvature of them such that when at rest the terminal segments now face the front of the fly.

The sclerites representing the abdominal segments distal to segment 8 are in male Syrphidae highly modified to form a genital capsule or *hypopygium*, incorporating a complex intromittent organ and accessory structures, together with the anus and its flanking cerci. The hypopygium is concealed beneath the terminal tergites of the preabdomen when at rest, in a hollow termed by Cole (1972) the genital pouch.

#### Male preabdomen

In species of genera such as *Melanostoma* and *Neoascia* there are distinct though minor differences in abdominal shape between males and females, produced by differences in the propor-

tions of tergites 1—4 (fig. 44). More subtle differences in the overall appearance of male and female abdomen occur in other genera, produced in the same way. Quite precise differences between male and female occur in the form taken by abdominal sternites in some genera, notably *Speghina*, *Neocnemodon* and *Eumerus*, where particular sternites of the male preabdomen exhibit structural modifications. The modifications may be in the form of sclerotised outgrowths along the mid-line, as in *Neocnemodon lattitarsis* (fig. 46) or paired lobes developed on the distal margin of some sternite, as in *Eumerus*.

#### Male postabdomen

Literature accounts of the degree of torsion exhibited by the abdomen of male Syrphidae are confusing, since in most instances it is stated that syrphids possess a *hypopygium inversum* or *b. retroversum*, but more recently it has been claimed they show the *b. circumversum* condition. The most explicit discussion of these conflicting views is found in Griffiths (1972: 56) as follows: Failure to appreciate the conceptual difference between rotation and deflexion has led to some confusion in the literature on Syrphidae, which I illustrate from the work of Zumpt and Heinz (1949). Zumpt and Heinz state that in *Eristalis*, "we are dealing with a *hypopygium inversum*, thus apparently contradicting the view (which I hold correct) that all Cyclorrhapha possess a *hypopygium circumversion*. However, if Zumpt and Heinz's arguments are followed closely, it will become apparent that they have confused rotational movement and deflexion. The hypopygium of *Eristalis* is "inverse" in the sense that it is so strongly deflexed that it points anteriorly and its "dorsal" side has become ventral."

To indicate the complex derivation of the orientation of the hypopygium found in Syrphidae, which his torsion theory demands, Griffiths (1.c.) suggests the term *hypopygium circumversum et reflexum* be used to describe the condition of the syrphid postabdomen. Lehrer (1971a) reached conclusions different again from those of Griffiths, dubbing the condition of the syrphid male postabdomen as a *hypopygium inverso-transversum*.

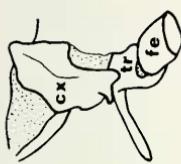
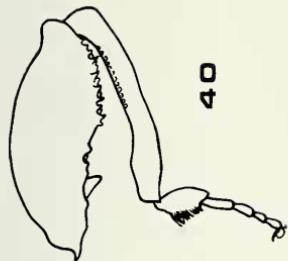
Whether the post-abdomen has twisted through 360° or 180°, the twisting has occurred anterior to the hypopygium. It is presumed to have occurred between segments, such that if a twist of 180° occurred between a given pair of segments, the *tergite* of the distal segment of the

pair would subsequently face outwards from the same surface as the *sternite* of the more proximal segment, and vice versa.

Griffiths' (1.c.) contention that a 360° torsion has occurred requires, in his view, a 180° twisting between segments 7 and 8 and a further 180° twisting between segment 8 and the hypopygium. The more traditional approach of Zumpt & Heinz (1949) contends that a 90° twist has occurred between segments 5 and 6 and a second 90° twist between segment 8 and the hypopygium. Lehrer (1.c.) suggests there has been 180° of torsion between abdominal segments 5 and 6, a further 90° of torsion between segment 8 and the hypopygium and a reflexion of the hypopygium from the longitudinal axis along which the segments up to and including segment 8 are aligned. He also points out that the hypopygium has in the latter process been pushed to one side.

In the present text, Griffiths' (1.c.) hypothesis of 360° torsion in the syrphid male postabdomen is regarded as unproven and the views of Zumpt & Heinz (1.c.) and of Lehrer (1.c.) are regarded as each in part correct. It is presumed that 90° of torsion has occurred between segments 5 and 6 and a further 90° between segment 8 and the hypopygium, leaving segments 6—8 on their sides and the hypopygium inverted. Subsequent reflexion of the postabdomen, progressively more complete from segment 7 onwards, has then led to the present state of the abdomen. The superfluity of complex — and different — Latinisms, each deemed to define precisely the *same* features of the male syrphid postabdomen, suggests that the practice of deriving such terms is a redundant exercise and no such term is employed here. Detailed discussion of torsion of the male abdomen in Diptera may be found in Griffiths (1972) and McAlpine (1981).

Abdominal segments 5—8 in Milesiinae and 6—8 in Syrphinae are much modified by the torsion process, going to form the "stalk" at the end of which is born the hypopygium. In both subfamilies tergites 6—8 remain reasonably large, externally visible sclerites, but the other plates involved are reduced to poorly sclerotised transverse strips concealed on or at the base of the "stalk". Zumpt & Heinz (1949) provide a clear illustration of these sclerites, suggesting that at the base of the stalk on the right side of the abdomen an extra, secondary, spiracle-bearing sclerite has been developed. This they term the "intersegmental sclerite". Lehrer (1971a) demonstrates that this "intersegmental sclerite" is part of tergite 5, joined narrowly to the other



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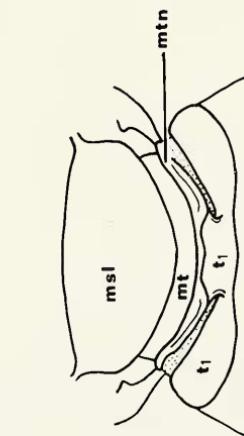
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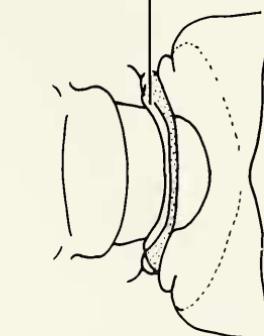
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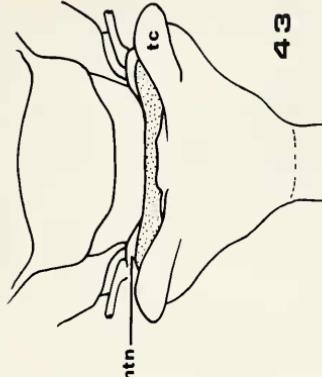


Fig. 38, *Platycheirus manicatus*, male, tarsomeres of left fore leg, dorsal view. Fig. 39, *Neocnemodon latitarsis*, male, base of left hind leg, lateral view of outer side. Fig. 40, *Syrphus ribesii*, left hind leg, lateral view of inner side. Fig. 41, *Syritta flaviventris*, junction between thorax and abdomen, dorsal view. Fig. 42, *Paragus bicolor*, junction between thorax and abdomen, dorsal view. Fig. 43, *Ceratina* sp., junction between thorax and abdomen, dorsal view.

elements recognised by Zumpt & Heinz (l.c.). Lehrer refers to these two elements of t.5 as hemitergites.

#### Male postabdomen: components of the hypopygium

Unfortunately, a favourite "sport" of syrphid morphologists and taxonomists has been to develop their own individual theories on the homologies of the component sclerites and structures of the hypopygium, and to accompany each theory with its own set of names for the sclerites involved. For instance, the main external plate of the hypopygium bears on its outer end a pair of appendages, to be seen on either side of, and just distal to, the cerci. These appendages have variously been called dististyli, gonopods, gonostyli, ninth coxites, paralobi, styli and surstyli. Matsuda (1976) points out that attempts to homologise sclerites of the male ano-genital complex of one family of Diptera with those either of the genitalia of other Diptera or of the original segments of the abdomen of Insecta in general are almost inevitably doomed to failure, because (a) they do not arise ontogenetically from homologous primordia in different families, and (b) secondary structures with no antecedents elsewhere are found repeatedly. It would thus appear that to attempt to name all parts of the syrphid hypopygium in such a way as to suggest precise homologies for the individual sclerites is by and large pointless. The names employed in this text for parts of the hypopygium are chosen from among existing terms which do not suggest particular origins for sclerites. This approach is the converse of that employed by McAlpine (1981).

When at rest tucked into the end of the pre-abdomen (figs. 47, 48) the most obvious feature of the hypopygium is the convex rim of a scoop-shaped sclerite (behind which the other structures are hidden from view) bearing the closely opposed cerci in a membranous cleft on its distal edge, which is oriented to point towards the head-end of the fly. This scoop-shaped sclerite is referred to here as the *basale*, which is joined round its basal rim to the distal rim of tergite 8. At the distal end of the basale, more or less flanking the cerci, are attached a pair of appendages here termed the *styli*. The styli are articulated to the basale rather than fused with it, and on the inner wall of the basale are continuous with a weakly sclerotised plate here called the *minis*. They may be simple, thumb-shaped pieces, as in *Eristalis* (fig. 51), or more complex structures with more than one lobe.

The main structure concealed within the basale when the hypopygium is at rest is the *theca*. The theca is essentially a sclerotised tube containing the aedeagus, but it usually carries sclerotised terminal lobes of some complexity which vary considerably in their form from species to species and genus to genus. The theca articulates to the inner edge of the basal rim of the basale. The terminal lobes of the theca are the *lingula* and the paired *superior lobes*. In its simplest form the lingula is a digitate or pointed projection, as in *Syrphus* (fig. 49). It may also be absent, as in *Eristalis* (fig. 51). The paired superior lobes may be either articulated to or fused with the main body of the theca. In many Syrphinae they articulate to cuticular outgrowths of the theca known as the *lateral arms* (fig. 49). In *Microdon* the theca is largely membranous and carries no structure that could be homologised with either lingula or superior lobes (fig. 50).

Three principal elements have been identified in the syrphid aedeagus. The most distal of these is the *tubus*, most often a weakly sclerotised, trumpet-shaped sclerite, which protrudes beyond the end of the theca (fig. 49). The tubus may be entirely lacking (e.g. in *Eristalis*, fig. 51). The tubus passes down into the *pyxis*, a roughly ring-shaped sclerite which sits in the mouth of the theca, with which its outer edge articulates. The pyxis may itself carry a pair of sclerotised, rather hook-like outgrowths known as the *harpes*, which often project from within the theca (fig. 51). Beneath the pyxis and articulated to it is the aedeagal apodeme, the tip of which is external and may be visible within the theca (fig. 49). *Microdon* again differs significantly from other hoverflies in possessing a pair of simple, whip-like sclerotised tubes as the sole aedeagal structures protruding from and contained within the theca. Metcalf (1921) recognised a structure deep within the hypopygium of *Microdon* as homologous with the pyxis of other syrphids.

This rather basic account of the principal components of the syrphid hypopygium falls far short of providing a reasonable indication of the range of variation they exhibit in different hoverflies. But in this one family of flies these structures exhibit a quite remarkable range of forms and the male genitalia of many syrphid species have been illustrated elsewhere recently: see Dusek & Laska (1964, 1967), Gaunitz (1960, 1966, 1969), Glumac (1960), Goeldlin (1976), Hippa (1968, 1978), Metcalf (1921), Thompson (1972), and Vockeroth (1969).

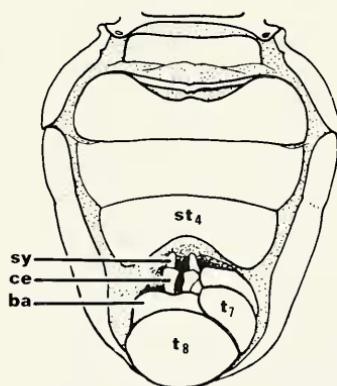
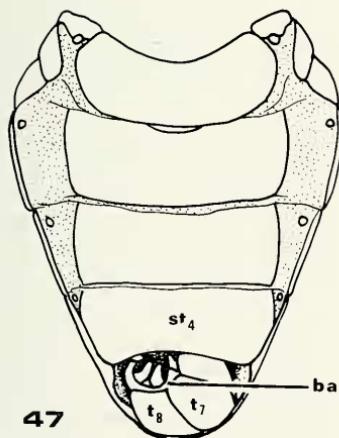
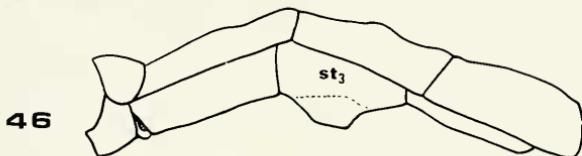
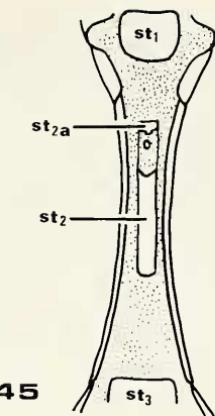
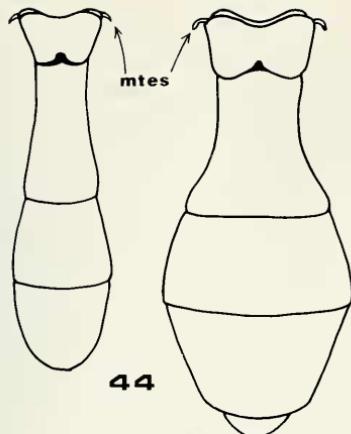


Fig. 44, *Neoascia podagraria*, male (left) and female (right), abdomen, dorsal view. Fig. 45, *Sphegina clunipes*, female, base of abdomen, ventral view. Fig. 46, *Neocnemodon latitarsis*, male, basal abdominal segments, lateral view, left side. Fig. 47, *Eristalis tenax*, male abdomen, ventral view. Fig. 48, *Microdon mutabilis*, male abdomen, ventral view.

### Female abdomen

Matsuda (1976) interprets the abdomen of female syrphids as comprising discernible elements of nine segments, plus the cerci. An alternative interpretation is provided by Lehrer (1971b), who follows Herting (1957) in identifying elements of ten segments plus the cerci. Matsuda (l.c.) points out that the nine segments he recognises cannot be assumed to be homologous in all dipteran families, because of the possibility that the particular segment which has been lost is not the same in all instances.

Both Lehrer (l.c.) and Matsuda (l.c.) agree in numbering the first eight visible abdominal segments of female syrphids from 1 to 8, sequentially, with each segment represented by a tergite and sternite. The first 7 segments each carry a spiracle. The spiracles lie in the membrane between tergite and sternite towards the anterior end of each segment, except in the case of the 1st abdominal spiracle, which is more frequently found entirely or partly enclosed within the posterior part of the metathoracic epimeron.

Beyond the eighth segment the situation becomes confused. Dorsally, Matsuda recognises a tergite 9 flanked by the cerci. Matsuda's tergite 9 is Lehrer's tergite 10 and the epiproct or proctiger of some other authors. For Lehrer, tergite 9 is identified with a pair of tiny lateral sclerites that are unconnected externally. These rudimentary plates are not mentioned by Matsuda.

Ventrally, Matsuda identifies in his text "the definitive 9th sternum or the postgenital plate as seen in *Eristalis*". He thus interprets this "postgenital plate" as sternite 9.

In the range of Syrphidae examined for purposes of the present account, the number of sclerites noted distal to the eighth tergite and sternite is not consistent. For instance, in *Syrphus* no dorsal sclerites distal to tergite 8 are found, although at least one additional dorsal sclerite distal to tergite 8 occurs in many other genera. Similarly, although in *Eristalis* a narrow sclerotised strip (st. 9 of Lehrer) occurs distal to sternite 8 and basal to the genital opening, this sclerotised strip is not present in other genera examined. Further, there are indications that secondary sclerotisation of membranous areas has on occasion occurred, as in *Eumerus* (fig. 55, ss).

What terminology to use for sclerites in the female abdomen posterior to tergite and sternite 8 is problematic. Lehrer's (l.c.) argument that the so-called "tergite 9" of Matsuda and McAlpine is in reality tergite 10 is persuasive. And if the

designation tergite 9 is retained for this plate, what are the small lateral sclerites regarded as tergite 9 by Lehrer? Authors other than Lehrer have conveniently ignored any mention of these lateral sclerites. Neither of the terms epiproct and proctiger can be used for the "tergite 9" of Matsuda and McAlpine because both have particular morphological connotations. Further, the morphological definition of these terms varies with author, as a comparison of the definitions in McAlpine and Tuxen (1970) demonstrates. Probably the most neutral of the available terms that have been applied to this sclerite in Diptera is the supra-anal plate, so that is what it has been termed here (see fig. 53 onwards, *sap*).

The pair of lateral sclerites regarded by Lehrer (l.c.) as derived from tergite 9 are not given any particular designation here. They are indicated in fig. 57 (fig. 57, *ls*). Lehrer was able to detect these sclerites in *Ceriana*, *Volucella* and *Xylota*, as well as in *Eristalis*.

Considering the ventral abdominal sclerites distal to sternite 8, *Eristalis* appears to be exceptional in exhibiting the sclerotised strip regarded by Lehrer (l.c.) as sternite 9. In the other species examined (including *Volucella bombylans* and *V. pellucens*) during preparation of this account the most that is visible in this position is a median, membranous flap which serves as an egg guide. Seeing the uncertain homology of this feature it is referred to here not as sternite 9 but as the ventral egg-guide (figs. 56 on, *vg*).

A pair of lateral sclerotised or membranous egg guides may also be present. They have been identified by Lehrer as elements of tergite 9. Since they are linked by a sclerotised bar passing along the upper margin of the genital opening, these lateral egg guides may be of sternal origin. The lateral egg guides are well exemplified by *Volucella* (fig. 58, *lg*). In *Eristalis* and *Sericomyia* the ventral egg-guide is well-developed but the lateral ones are lacking, while in *Syrphus* no egg-guides are differentiated (figs. 56—62).

The terminal ventral sclerite of the abdomen is the sternite 9 or post-genital plate of Crampton (1942), Matsuda (1976) and McAlpine (1981), which is sternite 10 of Lehrer (1971b). This plate appears to be universally present. Since its homology is questionable it is referred to here as the sub-anal plate (fig. 56 onwards, *sap*). The anus is located between the sub-anal plate and the supra-anal plate and is flanked by the cerci, which are generally recognised as being derived from the original eleventh abdominal

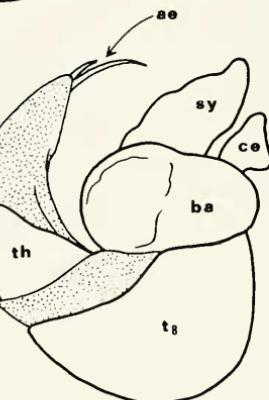
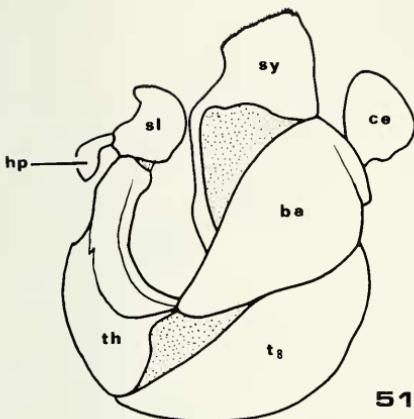
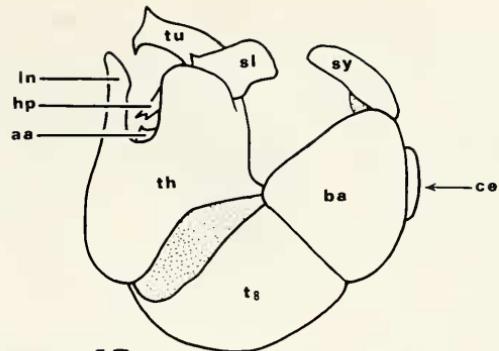


Fig. 49, *Syrphus ribesii*, male, hypopygium, lateral view. Fig. 50, *Microdon mutabilis*, male, hypopygium, lateral view. Fig. 51, *Eristalis tenax*, male hypopygium, lateral view.

segment. In *Syrphus*, where the supra-anal plate is lacking, the cerci come to occupy a mid-dorsal position (fig. 60).

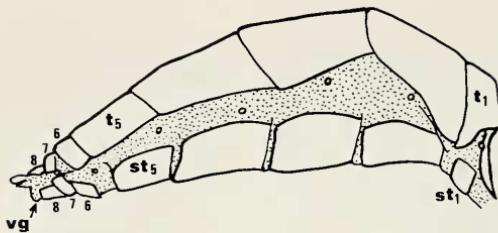
In many syrphids the abdominal segments posterior to segment 5 are hardly visible when at rest, being then retracted telescopically into segment 5, but they do not really form a distinct subregion of the abdomen as in the male. These terminal segments may be modified to form an ovipositor as long as or even longer than the first five abdominal segments together, the elongation being achieved primarily by widening the bands of intersegmental membrane, as in *Eristalis* and *Sericomyia* (figs. 53, 54). In *Eumerus* a similar result is achieved by elongation of the largely membranous segment 8. Also in *Eumerus*, secondary sclerotisation of the attenuated bands of intersegmental membrane has

produced a "false segment" between segments 6 and 7 and another "false segment" between segments 8 and 9. In the latter case a complete ring of sclerotised membrane has formed (fig. 55, ss).

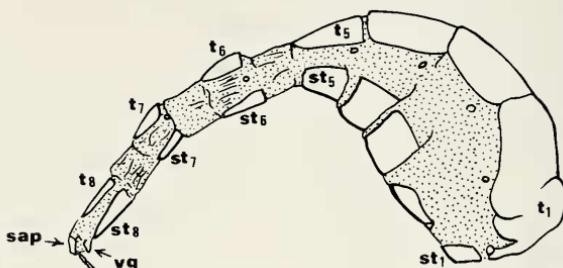
#### THE RELATIONSHIP BETWEEN THE SYRPHIDAE AND GENERA ALLIED TO *MICRODON*

Repeated references are made during course of this account to differences existing between the morphology of *Microdon* and the morphology of other syrphids. Various of these differences e.g. in *Microdon*'s mouthparts, have not been alluded to in other texts. *Microdon* and allied genera have until recently usually been regarded as constituting a separate subfamily, the Microdontinae, within the Syrphidae.

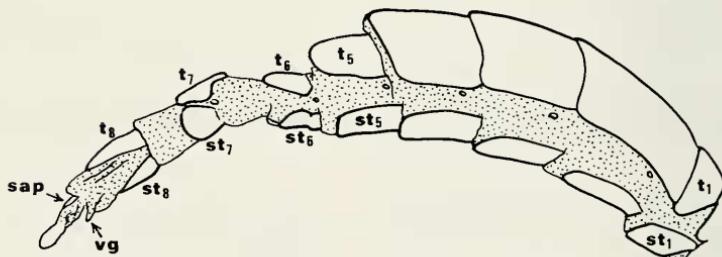
Thompson (1969) reviewed the genera con-



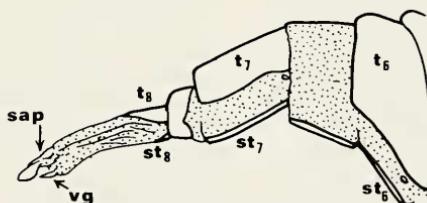
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53



54



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Fig. 52, *Syrphus ribesii*, female, abdomen, lateral view, right side. Fig. 53, *Eristalis tenax*, female, abdomen, lateral view, right side. Fig. 54, *Sericomyia silentis*, female, abdomen, lateral view, right side. Fig. 55, *Eumerus strigatus*, female, distal abdominal segments, lateral view, right side.

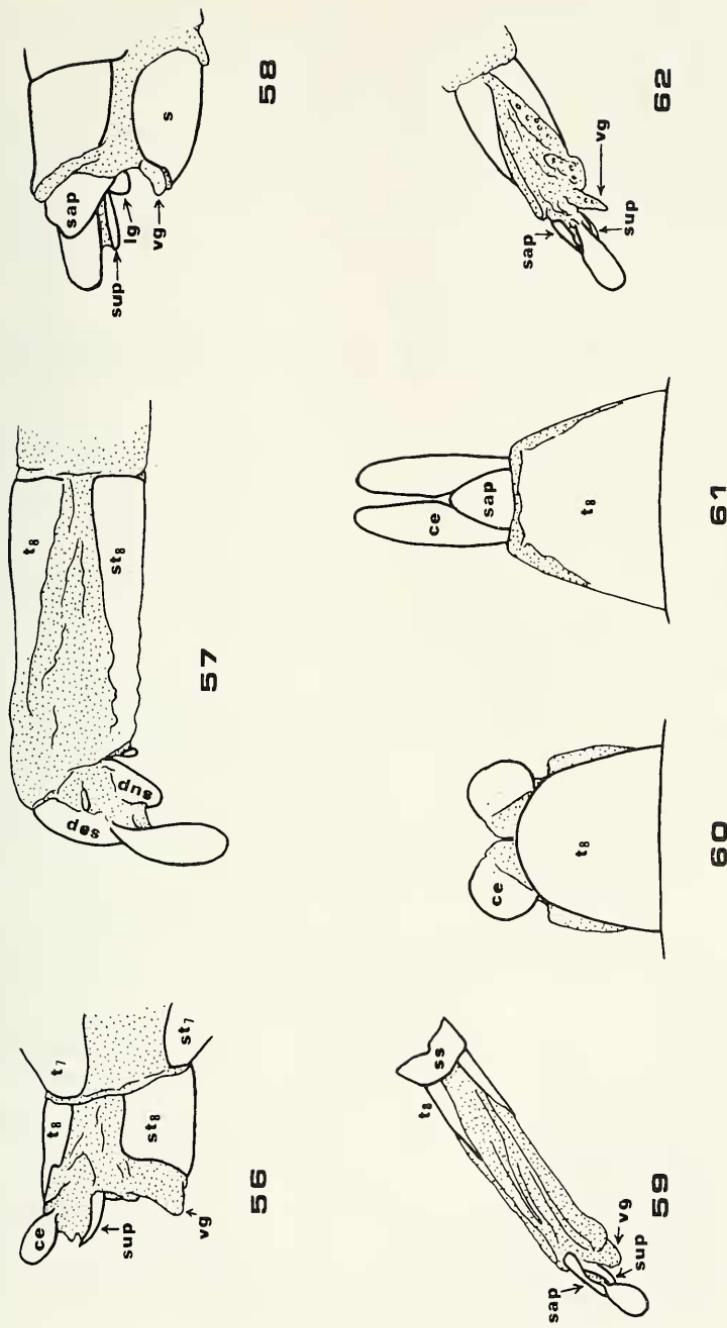


Fig. 56. *Syrbhus rihensis*, female, terminalia, lateral view, right side. Fig. 57. *Eristalis tenax*, female, terminalia, lateral view, right side. Fig. 58, *Eumerus strigatus*, female, terminalia, lateral view, right side. Fig. 59, *Syrbhus rihensis*, female, terminalia, lateral view, right side. Fig. 60, *Syrbhus rihensis*, female, terminalia, dorsal view. Fig. 61, *Microdon mutabilis*, terminalia, dorsal view. Fig. 62, *Sericomyia silenis*, terminalia, lateral view, right side.

signed to the Microdontinae and provided a definition of the subfamily, based upon both adult and larval characteristics. He concluded that "the Microdontines should be considered the first divergence in the phylogeny of the family (Syrphidae)". He further remarked that the "strongly plesiomorphic nature of the subfamily suggests that the microdons might best be considered as a separate family". In a later paper Thompson (1972) separated the Microdontidae from the Syrphidae. The additional data provided in the present account would tend to support Thompson's action, but does only relate to the European genus *Microdon*. If the other microdontine genera differ from the rest of the syrphids in these same ways, there would seem little justification for retaining the Microdontinae within the Syrphidae.

The incongruity attendant upon retention of the Microdontinae within the Syrphidae is highlighted by bringing into consideration the degree of morphological difference found between other dipteran groups currently recognised as separate families. However, Thompson's recognition of the family Microdontidae has not been adopted by other authors. For that reason *Microdon* has been included in this account of syrphid morphology, despite the present author's doubt that the genus belongs in the family Syrphidae.

#### ABBREVIATIONS USED IN FIGURES

a:	arista of antenna	bc:	buccal cavity
A:	first anal vein of wing	br:	barrette: probably the katepimeron of the mesothoracic pleura
aa:	aedeagal apodeme of aedeagus of male genitalia	bs:	prothoracic basisternum
ac:	anteclypeus	bt:	basitarsus of leg
ae:	aedeagus of <i>Microdon</i> male genitalia	C:	costal vein of wing
acs:	anterior cervical sclerite	ca:	presutural callus of mesonotum of thorax
acx:	anterior mesocoxite of middle leg	cal:	lower calypter of wing
al:	alula of wing	cau:	upper calypter of wing
am:	aristomere	cc:	cervical condyle of postoccipital sclerite
an:	anal cell of wing	ce:	cercus of terminal segment of abdomen
ans:	anapleural suture of mesothoracic pleura	cl:	claw of pretarsus of leg
as:	antecostal suture	cls:	clypeal sclerite in <i>Microdon</i>
at:	acrotergite of mesothoracic notum	co <sub>1</sub> , co <sub>2</sub> :	first and second costal cells of wing
att:	anterior tentorial pit	cs:	ceratostyle
au:	auxillia of pretarsus of leg	CuA:	anterior cubitus vein of wing
ax <sub>1</sub> , etc.:	axillary sclerite 1, etc.	CuP:	posterior cubitus vein of wing
b <sub>1</sub> , b <sub>2</sub> :	first and second basal cells of wings	cx:	coxa
ba:	basale of hypopygium of male genitalia	cxp:	posterior mesocoxite of middle leg
bat:	buccal arm of anterior tentorial sulcus	d:	discal cell of wing
		e:	compound eye
		em:	empodium of pretarsus of leg
		f:	face
		fe:	femur of leg
		fr:	frons
		frt:	frontal tubercle
		fs:	facial sulcus
		ft:	facial tubercle
		fu:	furca of labellum of labium
		g:	gena
		gl:	first segment of flagellum of antenna
		h:	hypopharynx
		ha:	haltere
		hb:	hypostomal bridge
		hc:	head capsule
		hr:	harpes of aedeagus of male genitalia
		hs:	hypostomal sulcus
		hu:	humeral cross-vein of wing
		hup:	humeral plate of wing-base
		hy:	hypoglossa of labium
		l:	lunule
		la:	lateral arm of theca of hypopygium of male genitalia
		lcs:	lateral cervical sclerite
		ll:	labellum
		In:	lingula of theca of hypopygium of male genitalia
		lr:	labrum
		lt:	lateral postnotal sclerite of mesonotum

M:	median vein of wing	pls:	pleural suture of mesopleura
M <sub>1—4</sub> :	branches of median vein of wing	pn:	postpronotal sclerite of pronotum
m:	marginal cell of wing	of thorax	
ma <sub>1</sub> , ma <sub>2</sub> :	anepisternites of mesothoracic	po:	posterior cell of wing
pleura	mesothoracic	pocb:	post-metaxocal bridge
map;	mesofurcal pit	ps:	proepisternum of propleura
mcu:	median-cubital cross-vein of wing	pu:	prothoracic furcasternum
mcx:	median mesocoxite of middle leg	R:	radial vein of wing
me:	mesepimeral sclerite of mesotho-	rm:	radial-median cross-vein of wing
racic pleura	racic pleura	Rs <sub>1—4</sub> :	branches of the radial-sector vein of
mhs:	median hypostomal suture	s:	the wing
mk:	katepisternum of mesothoracic	sa:	scape of antenna
pleura	pleura	sb:	subalar
mlt:	mesonotal prescutum	Sc:	band of sensilla on postgena
mn:	premental sclerite of the labium	sc:	subcostal vein of wing
mp:	mesosternal presternum	sca:	subcostal cell of wing
mr:	meropleurite of mesothoracic	scr:	postalar callus of mesonotum of
pleura	pleura	se:	thorax
ms:	mesoscutum of mesonotum	sen:	subcostal-radial cross-vein of wing
msl:	scutellar lobe of mesonotum	sep:	sella of cervical organ
mt:	median postnotal sclerite of me-	sl:	sensilla of cervical organ
sonotum		sm:	sensory pit of 3rd antennal seg-
mtb:	basisternum of metathoracic ster-	sp:	ment
nun:	nun	sps:	superior lobe of theca of male geni-
mte:	epimeron of metathoracic pleura	ss:	talia
mtec:	metepimeral callus of metathoracic	ssu:	submarginal cell of wing
pleura	pleura	st <sub>1</sub> , st <sub>2</sub> , etc.:	spiracle
mtes:	epimeral spine of the metathoracic	st:	spiracular sclerite of Microdon
pleura	pleura	thorax	
mtn:	metathoracic notum	ss:	secondary sclerite
mtpc:	precoxale of metathoracic pleura	ssu:	parasagittal sulcus of head capsule
mts:	episternum of metathoracic pleura	st <sub>1</sub> , st <sub>2</sub> , etc.:	sternum of first abdominal seg-
mtu:	furcasternum of metathoracic ster-	st <sub>2</sub> a:	ment, second abdominal segment,
nun:	nun	stg:	etc.
mua:	anterior mesosternal furcasternum	sy:	anterior sclerite of abdominal ster-
mub:	posterior mesosternal furcasternum	t <sub>1</sub> , t <sub>2</sub> , etc.:	nite 2
mvs:	mid-ventral thoracic suture	ta <sub>2</sub> :	stigma of wing
mx:	maxillary stylet	ta <sub>5</sub> :	stylus of basale of hypopygium of
mxa:	maxillary palp	tc:	male genitalia
oa:	ocular arm of anterior tentorial sul-	tg:	tergite of first abdominal segment,
cus		th:	second abdominal segment, etc.
oo:	post-ocular orbits	tho:	tarsal segments of leg
os:	orbital strip of face	ti:	callus of 2nd tergite of abdomen
osc:	post-occipital sclerite	tp:	tegula
ot:	ocellar triangle	tr:	theca of hypopygium of male geni-
p:	pedicel of antenna	trc:	talia
pa:	antepronotum of pronotum of	ts:	thorax
thorax		tt:	tibia of leg
pc:	postclypeus		posterior tentorial pit of head cap-
pcb:	premetaxocal bridge		sule
pcc:	postcranial carina		trochanter of leg
pcs:	posterior cervical sclerite		trochanteral process of posterior
pe:	proepimeron of propleura		mesocoxite of middle leg
pg:	postgena		transverse sulcus
			tempota of head capsule

tu:	tubus of aedeagus of male genitalia
u:	pulvillus of pretarsus of leg
v:	vertex of head capsule
vs:	vena spuria of wing
vv:	postvertex of head capsule

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